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PROCEEDINGS
OF THE
ROYAL SOCIETY OF VICTORIA

Volume 95

ROYAL SOCIETY'S HALL
9 VICTORIA STREET, MELBOURNE 3000

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DEVONIAN AND ?LATE SILURIAN PALAEOONTOLOGY OF THE WINNEKE RESERVOIR SITE, CHRISTMAS HILLS, VICTORIA

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ABSTRACT: During construction of the Winneke Reservoir a number of Late Silurian or Early Devonian fossils were discovered in the Dargile-Humevale Formation transition beds and as all the sites are now underwater, description of these fossils is presented as most are first records for Australia. They include a species of scyphomedusoid, *Conularia comriei* sp. nov. the trilobites *Odontochile formosa* Gill 1948, *Reedops* sp. nov. and a questionable record of the Subfamily Tropidocoryphinae, the crinoids *Dendrocrinus saundersi* sp. nov., *Codiocrinus rarus* sp. nov., *Kooptoonocrinus nutti* gen. et sp. nov., and a new genus of Dimerocrinitidae, the solutan carpoid *Rutroclypeus junori* (Withers 1933) and the ophiuroids *Urosoma glabridiscus* Talent 1965 and *Mausoleaster sugarloafensis* gen. et sp. nov. Apart from the new genera it is the first Australian record for *Reedops*, *Codiocrinus* and *Dendrocrinus*.

When the Winneke Reservoir filled in 1981 the area drowned was underlain by Upper Silurian and/or Early Devonian sediments of the Dargile and Humevale Formations. Considerable earthworks including quarrying for rock fill during construction of the dam afforded excellent exposures of fresh rock. Fossils proved to be relatively rare in the exposed sediments but are nevertheless quite significant in several respects.

One site NMVPL261 yielded enormous numbers of the large dalmanitinid trilobite *Odontochile formosa* but only five specimens of *Reedops*, one of the carpoid *Rutroclypeus junori* and one of the ophiuroid *Mausoleaster sugarloafensis*. NMVPL260 on the other hand produced large numbers of brachiopods but only a single echinoderm. Taken overall the seven echinoderm species are known from only 10 specimens whereas one trilobite species is known from hundreds. The lithologies of the collecting localities are not vastly different, suggesting that conditions were similar. Such radically different faunas from similar sites, thought to be relatively close together temporally, suggest that they are not natural assemblages. Moreover, articulated trilobites and whole echinoderms suggest burial of live animals. Taken together these two indications suggest some sort of mud flow deposition.

The fauna itself provides several new generic records for Australia particularly among the echinoderms, new information on *Rutroclypeus* that shows its stèle to have a structure much more in keeping with other solutan carpoids than was previously acknowledged, a firmer understanding of the species *Odontochile formosa*, and the first Australian record of *Reedops*.

All material is housed in the Palaeontological Collections of the National Museum of Victoria (prefixed NMVP) and localities appear on the Palaeontological Locality register of the same institution (prefixed NMVPL).

LOCALITIES

The Winneke Reservoir is situated 33 km northeast of Melbourne, just south of Christmas Hills on the Wat-

son's Creek to Yarra Glen Road (Fig. 1, inset). Fossils were recovered between 1979 and 1981 from the two now-flooded localities NMVPL260 & 261 (Fig. 1).

NMVPL261 was a low cutting for an access track on the right bank of the stream gully not far above the stream level; Yan Yean 1:63 360 geological sheet, grid reference 500298. Fossil list:

Trilobita	<i>Odontochile formosa</i> Gill 1948 <i>Reedops</i> sp. nov. Tropidocoryphinae? gen. et sp. indet.
Mollusca	straight nautiloid indet.
Coelenterata	solitary Rugosa (moulds only) <i>Conularia comriei</i> sp. nov.
Echinodermata	<i>Rutroclypeus junori</i> Withers 1933 <i>Mausoleaster sugarloafensis</i> gen. et sp. nov.
Brachiopoda	<i>Notoparmella plentiensis</i> Garratt 1980

NMVPL260 was in a small cutting for a track that ran up the side of the ridge from the main creek gully; Yan Yean 1:63 360 geological sheet, grid reference 501295. Fossil list:

Echinodermata	<i>Codiocrinus rarus</i> sp. nov.
Brachiopoda	<i>Notoparmella plentiensis</i> Garratt 1980 <i>Notanoplia panifica</i> Garratt 1980

Site geologists Ray Saunders and Wayne Regan made a collection during initial excavations at a site now buried beneath the right abutment of the main dam wall, which is situated at grid reference 493293 on the Yan Yean 1:63 360 geological sheet. Fossil list:

Echinodermata	<i>Dendrocrinus saundersi</i> sp. nov. <i>Mausoleaster sugarloafensis</i> gen. et sp. nov. <i>Urosoma glabridiscus</i> Talent 1965
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The only other fossils described are on a single slab of siltstone that was removed from a quarry at the dam site to a distant location. At the time of dumping Mr.

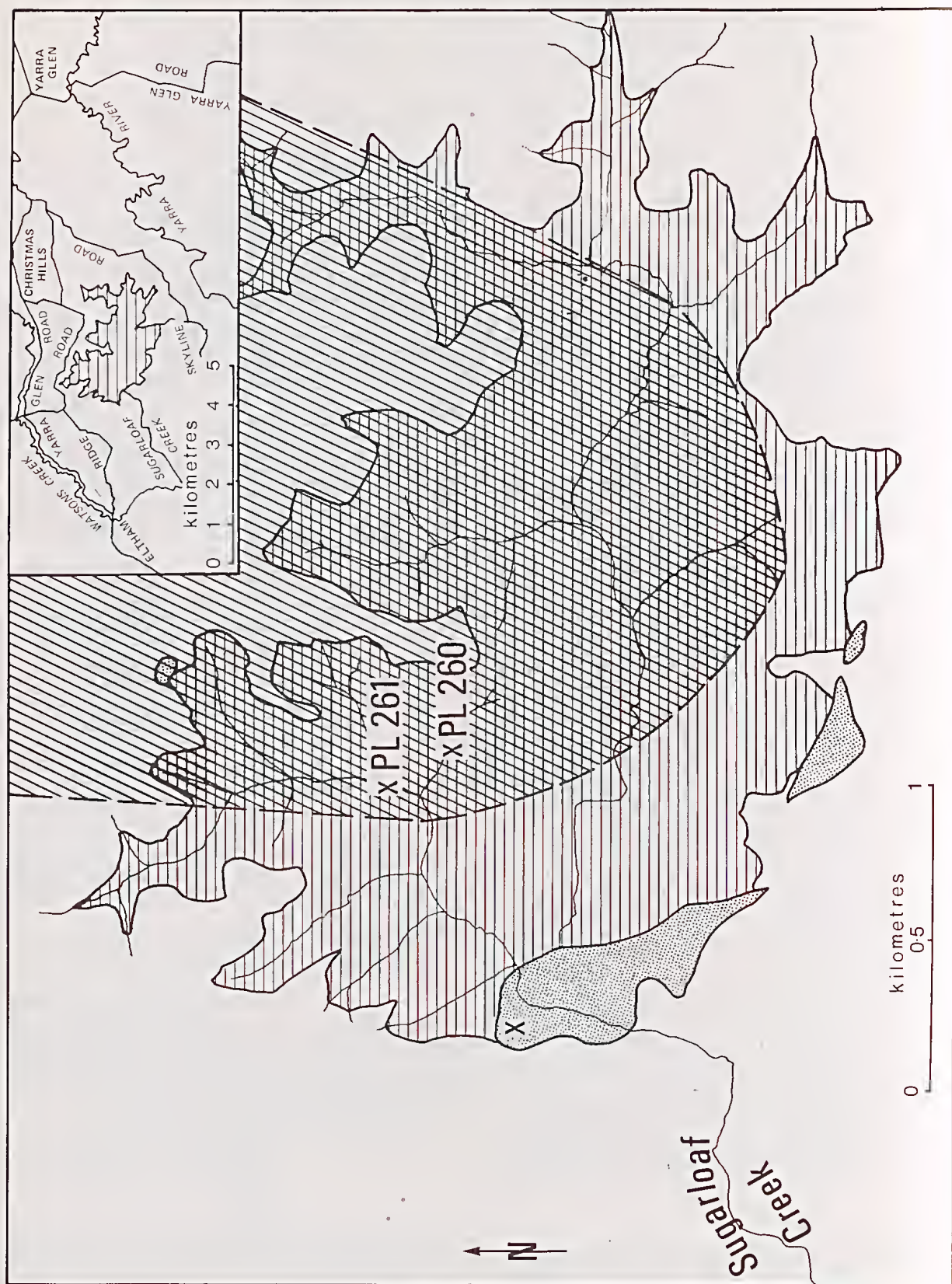


Fig. 1—Locality map. The dam walls are stippled and the flooded area is horizontally lined (in the inset also). The horizontal lines in the inset are horizontally lined (in the inset also). The horizontal lines in the inset are horizontally lined (in the inset also).

Ron Nutt split the rock exposing two crinoids identified as *Kooptoonocrinus nutti* gen. et sp. nov. and *Dimerocrinitidae* gen. et sp. nov.; as a consequence the exact site and horizon of the specimens are not certain. Fossil fragments were noted at a number of other localities within the dam site but no specimens were complete enough or well enough preserved for identification.

STRATIGRAPHY AND AGE

On the Yan Yean 1:63 360 geological map the strata at the site of the main dam wall are assigned to the Dargile Formation of Ludlovian age. None of the fossils from the site contradict this age, and in fact one of the species, *Urosoma glabridiscus* Talent 1965, was originally described from the type area of the Dargile Formation in the Heathcote district, where it occurs at a similar stratigraphic level as early Ludlow graptolites (VandenBerg & Garratt 1976). Localities NMVPL260 and 261 lie close together stratigraphically much higher in the sequence than the site of the dam, but there has been some confusion as to their exact age and horizon. On the Yan Yean 1:63 360 geological map they are situated just above the base of the Humevale Formation which is shown as corresponding with the Silurian-Devonian boundary, although in the Clonbinane area some 45 km to the northwest the Humevale Formation is now known to extend down into the Ludlow (Garratt 1978). Garratt (1980) assigned the strata at NMVPL260 to the upper part of the Dargile Formation and suggested a late Ludlow-Pridolian age, based on the presumed ages of the strata at other localities in the Melbourne Trough where *Notoparniella plentiensis* and *Notanoplia panifica* are known to occur. However, the fossils we describe from NMVPL261 suggest that the age may be somewhat younger than this. *Odontochile formosa*, *Conularia comriei* and *Rutroclypeus junori* all occur quite high in the Humevale Formation at Kinglake West, where the sediments are of Early Devonian age. Of course these species may be long-ranging, but more compelling evidence for an Early Devonian age is provided by *Reedops* sp. nov. The oldest known species of this genus is *R. deckeri* Delo 1935 from the Gedinnian of Oklahoma, and the next oldest species are all early Siegenian (Campbell 1977).

SYSTEMATIC PALAEONTOLOGY

Phylum COELENTERATA (P.A.J.)

Class SCYPHOZOA

Order CONULARIIDA Miller & Gurley 1896

Family CONULARIIDAE Walcott 1886

Geus *Conularia* Sowerby 1821

Conularia comriei sp. nov.

Fig. 2

ETYMOLOGY: The species is named for Mr. Michael

Comrie, who, as site manager for the reservoir project, greatly facilitated our collecting.

HOLOTYPE: The external mould NMVP74247 of an incomplete specimen from NMVPL261.

PARATYPES: NMVP79546 from a small quarry on the Whittlesea road 3.2 km from Kinglake West, and NMVP73828 from NMVPL261.

DESCRIPTION: The individual was very large (80 mm long and incomplete); regular transverse ridges (21 per 10 mm) bear prominent tubercles which are not continuous across the interridge spaces but do line up in longitudinal regular columns; the transverse ridges are continuous across marked corner depressions; tubercles on the transverse ridges become quite crowded together in the corner depressions and become elongate off the ridges into the interridge spaces which they cross completely at many levels. On the faces, the transverse ridges very rarely bifurcate (3 examples known, see Fig. 2A, B, D).

REMARKS: The holotype is larger than almost all described conulariids. The state of preservation with the two surfaces crushed against each other and a great deal of fragmentation suggests that the wall was relatively soft and, unlike that of most other conulariids, had little mechanical strength. Towards the apical end (i.e., down in Fig. 2C) are two long tapering scimitar-shaped objects that project from inside the ruptured individual. Such objects are common throughout the Silurian and Devonian of the Melbourne Trough but are generally not associated with conulariids. If they are not part of the conulariid it is difficult to imagine how they became lodged where they are in what are apparently rapidly buried fossils. It may be that they are part of an organism that scavenged on and caused the extensive fragmentation of walls evident at that end of the conulariid. This association is ambiguous but may hold a clue to the identity of the relatively common scimitar-shaped fossils.

The bifurcations (or discontinuities) of certain transverse ridges forming a loop in one case (Fig. 2D) are rare in conulariids outside the corners and midlines. Their significance is not apparent as functional interpretation of conulariids has not yet been accomplished.

This species is readily distinguished from *C. ornaticissima* Chapman 1903 (see Talent 1965) by its fewer ridges per unit length and by its size; from *C. chapmani* Fletcher 1938 by its discontinuous longitudinal columns, size and occasional ridge bifurcations; from *C. sowerbyi* de Verneuil 1845 by its size, by its tubercles not being so close packed, and by its tubercles being in longitudinal alignment. It should be noted in passing that neither of the Victorian specimens attributed to *C. sowerbyi* by Chapman (1903) belongs to *C. chapmani* as suggested by Fletcher (1938); they each represent separate species. Talent's (1965) *Conularia* n. sp. appears to be conspecific with *C. comriei* but its very fragmentary nature precludes certain identification.

Phylum ARTHROPODA (D.J.H.)

Class TRILOBITA

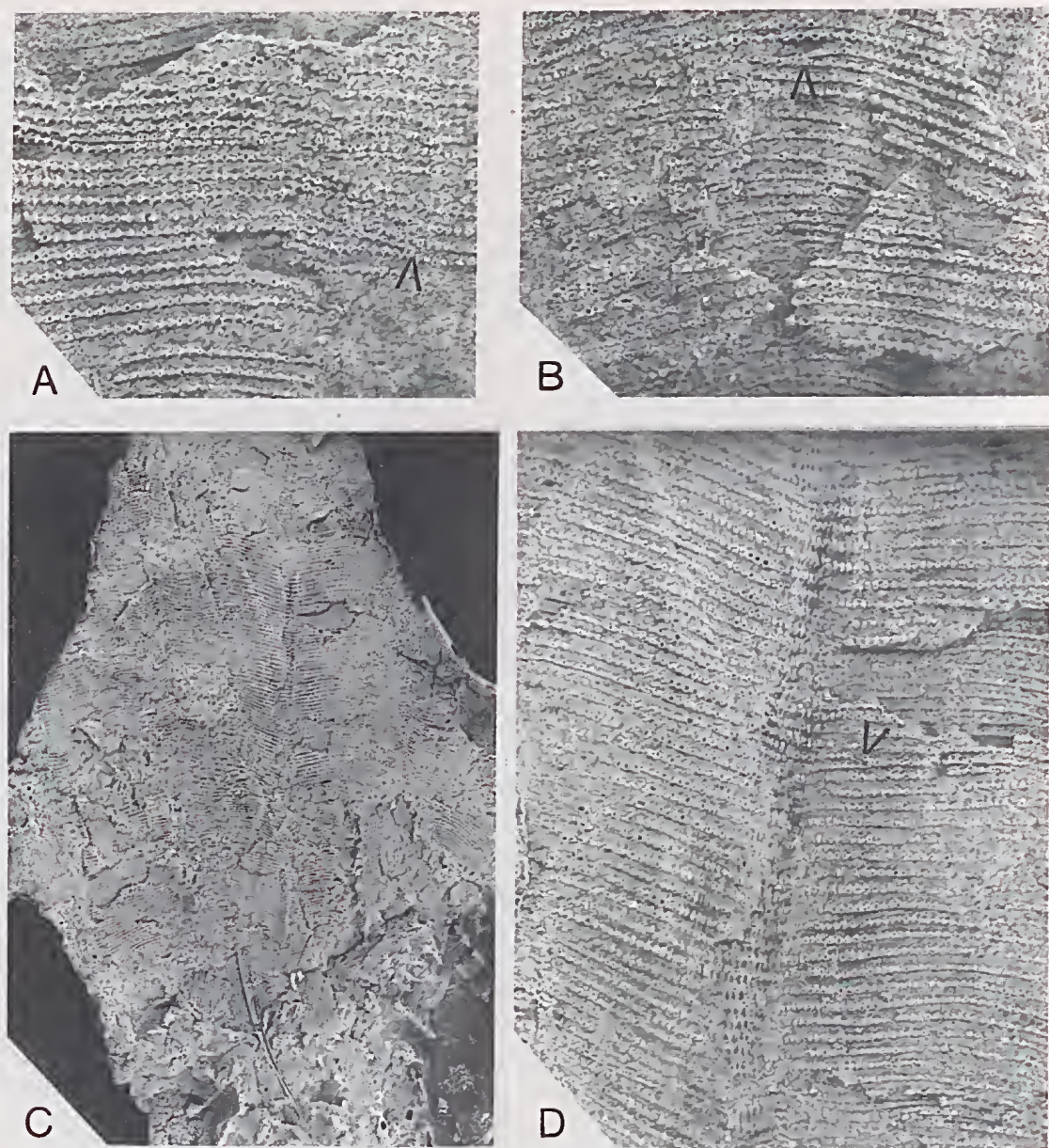


Fig. 2—*Conularia comriei* sp. nov. NMVP74247. A, B, D, enlargements of latex cast of various parts of specimen fully illustrated in C; arrows indicate bifurcations in the transverse ridges, A, B, $\times 6$; D, $\times 4$; C, $\times 1$.

Order PROETIDA Fortey & Owens 1975

Superfamily PROETACEA Salter 1864

Family PROETIDAE Salter 1864

Subfamily TROPIDOCORYPHINAE Pribyl 1946

Tropidocoryphinae? gen. et sp. indet.

Fig. 3I

MATERIAL: An incomplete thorax and pygidium from NMVPL261.

REMARKS: The most distinctive features of the pygidium are the narrow axis (the axial rings themselves are not preserved); the pleural furrows that are sharply impressed, except for the posterior two, and have steep anterior slopes and gentle posterior slopes; the non-existent interpleural furrows; the anterior pleural bands that are elevated above the posterior bands, especially distally; the very narrow border on the pleurae; and the ornament of fine striations. The specimen is tentatively assigned to the Tropidocoryphinae because the structure of the pygidial pleurae is similar to the imbricate type found in that subfamily.

Order PHACOPIDA Salter 1864

Suborder PHACOPINA Struve in Moore 1959

Superfamily PHACOPACEA Hawle & Corda 1847

Family PHACOPIDAE Hawle & Corda 1847

Subfamily PHACOPINAE Hawle & Corda 1847

Genus *Reedops* R. & E. Richter 1925

TYPE SPECIES (by original designation): *Phacops bronni* Barrande 1846 from the Dvorce-Prokop Limestone (Pragian) at Damil near Tetín, Czechoslovakia.

REMARKS: This genus has been discussed recently by Campbell (1977) and Chlupáč (1977).

Reedops sp. nov.

Fig. 3A-H

MATERIAL: Two incomplete cephalae, an incomplete thorax, and two thoraces with pygidia attached, from NMVPL261.

DESCRIPTION: Glabella very incomplete on available cephalae. Occipital ring with well-defined lateral lobes 0.5 times as long (exsag.) as medial portion of ring. Lateral nodes of 1p lobe distinctly larger than occipital lobes; 1p furrow directed posteromedially as far as inner edge of node where it shallows abruptly and is deflected forwards. Sides of glabella diverge at approximately 60° in front of 1p furrow; 2p and 3p furrows very weak, 2p apparently situated level with posterior edge of eye, 3p with convex-forward inner part lying opposite midlength of eye and outer part converging gently with axial furrow at front of palpebral lobe. Cheek is gently convex in transverse and lateral profiles and slopes steeply anterolaterally. Eye situated well forward and low on cheek, with ventral margin lying in lateral border furrow; distance of eye from junction of lateral and posterior border furrows almost equal to its own length. Palpebral lobe relatively narrow, with outer rim defined by shallow marginal furrow; palpebral furrow only weakly curved and continuous posteriorly with a deeper postocular furrow. Visual surface composed of at least 21 dorsoventral lens files of up to 13 lenses each; lenses very closely spaced so that each is almost in contact with its neighbours, even at top of files. Posterior border well-rounded (exsag.) proximally, expanding abaxially beyond the fulcrum and becoming more flattened; posterior border furrow deep and sharp. Lateral border steeply inclined, narrowing slightly from genal angle to posterior edge of eye; lateral border furrow decreases in depth where it is deflected outwards around base of eye. Entire dorsal surface of cephalon (except in furrows) covered with coarse granules ranging in diameter from 0.2 mm to less than 0.1 mm. Finest granules on glabella are just above preglabellar furrow, and densest concentration is on upper surface of frontal lobe. On cheek, granules decrease in size and density adjacent to axial furrow and on lateral border beneath eye; outer rim of palpebral lobe is densely covered with fine granules.

Lateral part of cephalic doublure carries a deep, weakly notched vincular furrow bounded on the inside by a prominent, sharp ridge that weakens opposite posterior edge of eye. Posteriorly, vincular furrow is deflected inwards across doublure towards distal end of posterior border furrow, and anteriorly it shallows abruptly beneath midlength of eye (the sharp line extending forward from this position in Fig. 3E is a crack). Medial part of doublure incompletely known, but fragments preserved show that anterior part of vincular furrow is long (sag., exsag.), weak and poorly defined, and carries normal ornament (Fig. 3H, arrowed). Ornament on doublure consists of granules that are smaller than those on dorsal surface, and that develop laterally into fine terrace lines on ridge along inside of vincular furrow. Inner, flattened part of doublure below this ridge is smooth.

Thoracic segments have strongly arched (tr.) axial rings with well-developed lateral nodes, and pleurae that rise gradually from axial furrow to fulcrum where they are turned strongly downwards. Axial rings contract slightly medially; in lateral profile they are rather flat-topped posteriorly but curve strongly downwards anteriorly into a deep, sharp articulating furrow that is slightly recessed below front of ring. Pleural furrows sharply impressed, with short, abrupt anterior slopes and more gradual posterior slopes; abaxially they curve forwards slightly onto articulating facets. On anterior segments, pleura curves gently forwards beyond fulcrum to broadly rounded tip; on posterior segments abaxial part of pleura is straighter and tip is almost orthogonally truncated. Doublure beneath pleural tips has well-developed panderian protuberances that are more oblique on anterior segments than posterior segments, and on posterior and distal margins of doublure are ventral projections that during enrollment overlap distal edge of succeeding segment (Fig. 3G). Granules on axial rings (excluding lateral nodes) and on downturned portion of pleurae beyond fulcrum are similar to those on glabella; on axial nodes and proximal portion of pleurae they are finer and less dense. Pleural doublure seems to be smooth.

Pygidium with 9 axial rings successively decreasing in convexity (sag., exsag.) posteriorly; small pseudo-articulating half rings present on rings 2 and 3, and tiny vestiges of them possibly remaining on rings 4 and 5. Ring furrows 1 to 4 deep and sharply impressed, but subsequent ones much shallower; all except posterior few ring furrows have transverse medial portions and lateral portions that are deflected forwards slightly and are weakly concave backwards. There are 7 or possibly 8 pleural furrows, the first four deep and sharp, and the last few very weak; there are 4 interpleural furrows that are shallow but distinct and do not extend as far abaxially as pleural furrows. Doublure consists of inner and outer bands that are concave in cross-section and separated by a marked change of slope that swings sharply inwards anteriorly across doublure. Inner band more steeply inclined than outer band, more concave (tr.) and wider, except posteriorly where it contracts

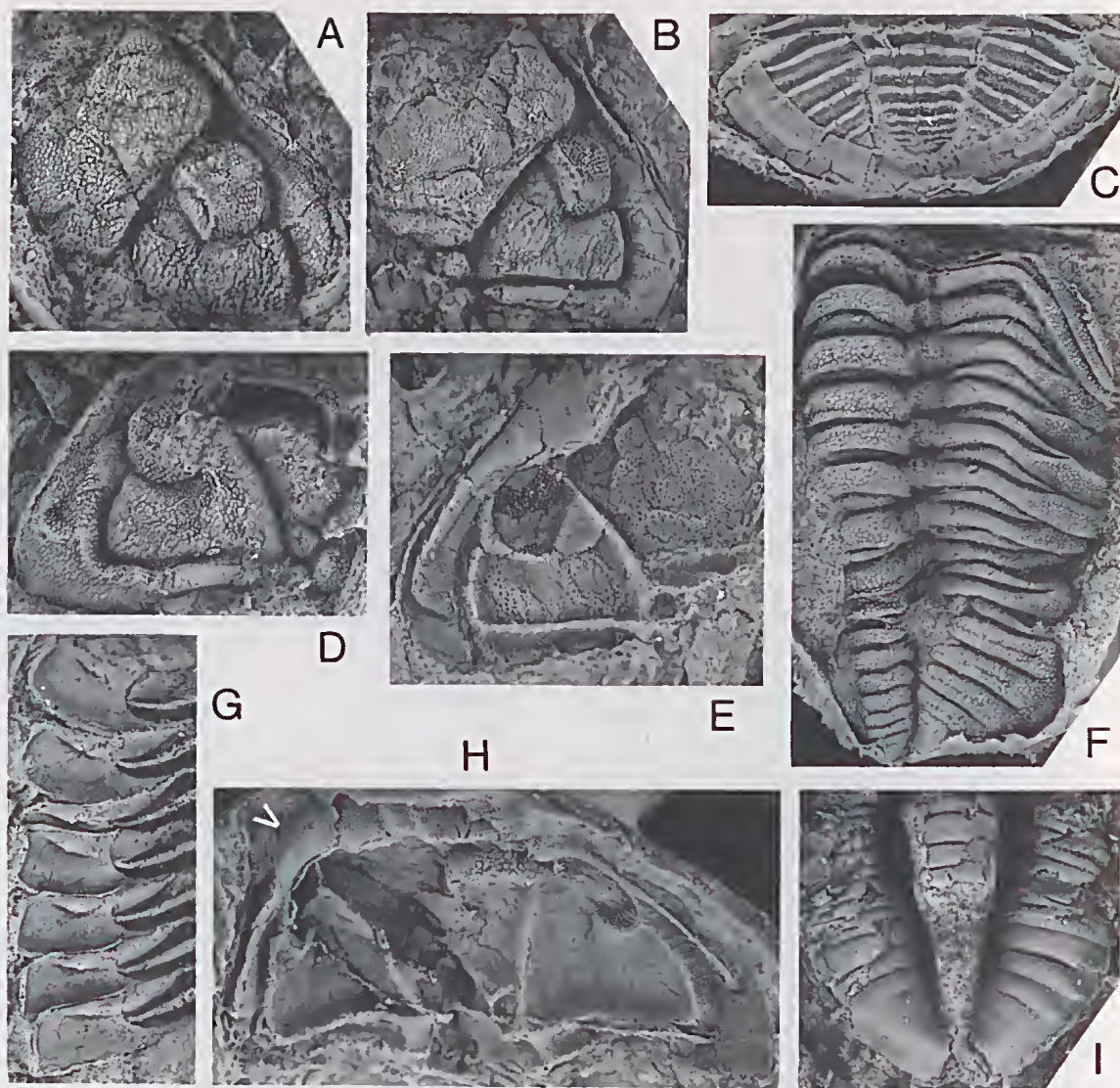


Fig. 3—A-H, *Reedops* sp. nov. All photographs except B are of latex casts. A, B, E, cephalon NMVP 82779, $\times 2$; A, E, dorsolateral and ventral views; B, internal mould in dorsal view prior to preparation to expose external mould of doublure. C, pygidium of specimen with articulated thorax NMVP82780, ventral view, $\times 1.8$. D, H, cephalon NMVP82781; D, dorsolateral view, $\times 2.5$; H, ventral view, $\times 2.2$ (arrow indicates very weak anterior portion of vincular furrow; note that coarsely granulated object just behind doublure in centre of photograph is axial ring of a displaced thoracic segment). F, thorax and pygidium NMVP82782, dorsolateral view, $\times 2.2$. G, pleural tips of incomplete thorax NMVP82783, ventrolateral view, $\times 2.5$ (anterior at top of photograph). I, *Tropidocoryphinae*? gen. et sp. indet. NMVP82784. Dorsal view of incomplete thorax and pygidium with exoskeleton preserved, $\times 5.3$.

gradually behind axis. Granules on dorsal surface of pygidium similar to those on glabella; granules on doublure much finer.

REMARKS: This species is clearly a member of *Reedops*, as shown by the rather uniform size of the granules over the entire exoskeleton, including the glabella; the relatively small, anteriorly placed eye that lies with its lower edge in the lateral border furrow; the very weak 2p and 3p furrows; and the vincular furrow that is deep

laterally but almost non-existent medially. In the coarseness of the exoskeletal granulation and the deep axial and pleural furrows on the pygidium, it is most similar to *R. deckeri* Delo 1935 from the Gedinnian of Oklahoma (Campbell 1977). It differs from that species, however, in having eyes that are shorter (exsag.) but have a greater number of lenses per dorsoventral file, more weakly curved palpebral furrows, weaker furrows 2p and 3p, and a more poorly defined medial notch in the inner edge of the pygidial doublure.

Superfamily DALMANITACEA Vogdes 1890

Family DALMANITIDAE Vogdes 1890

Subfamily DALMANITINAE Vogdes 1890

Genus *Odontochile* Hawle & Corda 1847

TYPE SPECIES (ICZN Opinion 537 (1959)): *Asaphus hausmanni* Brongniart 1822 from the Dvorce-Prokop Limestone (Pragian), Prague district, Czechoslovakia.

Odontochile formosa Gill 1948

•Fig. 4

1948 *Odontochile formosa* Gill, p. 20, pl. 2, figs 1, 2.
TYPE MATERIAL: Holotype Melbourne University Geology Department 882, internal mould of very large, almost complete dorsal exoskeleton from quarry approximately 2.8 km southwest of Kinglake West, Victoria (vicinity of locality W1 on map of Williams 1964, fig. 2); Humevale Formation (Early Devonian).

OTHER MATERIAL: Abundant remains of cephalon, thoraces, pygidia and hypostomes, mostly disarticulated and broken, from NMVPL261.

DESCRIPTION: Glabella expanding strongly forwards, widths at occipital ring, 3p lobe and frontal lobe approximately in ratio 1:1.5:2. Occipital ring well-rounded in lateral profile; in transverse profile it is strongly convex medially but becomes gently concave abaxially; no median occipital tubercle. Occipital furrow moderately deep medially, deflected gently backwards abaxially and becoming sharper as it turns down into occipital apodeme, finally curving laterally or even slightly forwards distally. Apodemal pits 1p and 2p directed slightly obliquely backwards abaxially, connected to axial furrow by distinct furrows 1p and 2p, and tending to be joined medially across glabella by shallow transverse furrows. 3p furrow deep, inner portion gradually increasing in length (exsag.) abaxially, outer portion expanded, more oblique than inner portion and more evenly curved in cross section (exsag.). Glabellar lobe 1p convex (tr.) medially but rising fairly steeply towards its anterolateral extremities; lobes 2p and 3p with inflated abaxial portions separated from gently convex (tr.) medial portions by broad and poorly defined longitudinal furrows. Frontal lobe approximately 1.6 times as wide as long, comprising more than half glabellar length and bearing a shallow longitudinal depression medially in its posterior half. Preglabellar furrow shallow abaxially and not impressed medially.

Palpebral lobe in most specimens situated further from sagittal axis posteriorly than anteriorly, distance from posterior border furrow slightly greater than length (exsag.) of posterior border; palpebral furrow shallowest in its posterior half. Eye with lenses arranged in approximately 50 dorsoventral lens files of up to 14 lenses each. Beneath eye is strongly impressed furrow, along outside of which on librigena is a prominent rounded (tr.) eye platform abutting lateral border furrow. Anterior branch of facial suture lies close to axial

and prelabellar furrows, diverging strongly from γ to β ; from ϵ , posterior branch of suture runs just outside furrow beneath eye, before curving in a broad arc across cheek so that ω lies opposite 2p lobe. Anterior border of cephalon decreases slightly in length (sag., exsag.) adaxially, median process absent. Lateral border with epiborder furrow more distinct on librigena than on fixigena; lateral border furrow shallow and well-rounded in cross section on librigena but sharper on fixigena. Posterior border expands distally to more than twice its proximal length (exsag.). Genal spine rather long and slender.

Granular ornamentation very sparse over most of dorsal surface of cephalon, but more dense on posterior and median parts of occipital ring, on central part of frontal lobe, on anterior border, and on palpebral lobe. (On the latter, granules increase in density towards the lateral margin but decrease in size.) Ornamentation not preserved on lateral and posterior borders and on dorsal surface of genal spine.

Hypostomal suture gently convex forwards. In front of hypostomal suture doublure gradually expands adaxially and is crossed by a deep arcuate depression running subparallel to cephalic margin; lateral to hypostomal suture doublure narrows slightly abaxially in front of eye and has a very low, upturned inner flange lying directly beneath eye platform. Posterior branch of facial suture runs backwards across doublure in a slight curve, meeting inner margin beneath distal end of posterior border furrow. Hypostome approximately as wide across anterior wings as long (sag.). Anterior border expands strongly towards anterior wings and anterior border furrow is very weak. Lateral margin curves sharply outwards from anterior wing to prominent shoulder lying well in front of hypostomal midlength. Behind shoulder, lateral border decreases in height and width, and lateral border furrow converges only weakly until level with medial part of middle furrow, where border becomes more flattened and expands gradually, and border furrow shallows and curves inwards. Posterior border has a shallow transverse, arcuate furrow running close to posterior margin, the latter deflected backwards medially and abaxially to three small spines; lateral border furrow contains a pair of indistinct depressions directly in front of lateral pair of spines. Outer portion of middle furrow meets lateral border furrow opposite shoulder and runs obliquely backwards to a pair of depressions lying just behind the hypostomal midlength; medial portion of middle furrow transverse, shallower than outer portion. Maculae not observed. Cephalic doublure (with possible exception of inner flange) and hypostome densely granulate.

Thorax composed of 11 segments. Axis increases in width (tr.) only weakly on first three segments and narrows just as weakly on last six segments; axial rings rather flattened (sag., exsag.), contracting slightly medially and tending to be orthogonally truncated by axial furrow distally. Pleural tips not well preserved on more anterior segments; posterior segments curve backwards distally to a sharp point. Doublure on

pleurae of posterior segments broad (tr.), inner edge subangular in outline (Fig. 4I, K); no trace of any pandermanian protuberance.

Pygidium approximately as wide as long (including mucro) in relatively undistorted specimens; lateral margin gently curved but overall outline is subtriangular rather than semielliptical. Axis 0.2 times as wide as pygidium anteriorly and narrowing uniformly backwards, composed of 17-19 or possibly 20 axial rings plus a terminal piece. Successively diminishing pseudo-articulating half rings are developed on at least rings 2-8, and in some specimens oblique muscle impressions are present on posterior half of rings lateral to pseudo-articulating half rings (Fig. 4B); ring furrows very short (exsag.) and sharp abaxially but longer sagittally and weak, even near front of axis. There are 13-14 pleural furrows that are evenly curved on more anterior segments but almost straight on posterior ones. Pleural furrows expand slightly distally and become shallower but extend virtually to pygidial margin; interpleural furrows terminate well inside margin. Mucro slender and extended horizontally backwards; its length measured from axial terminus is approximately half length of axis. Doublure gently convex (tr.), lacking a steeply inclined inner flange.

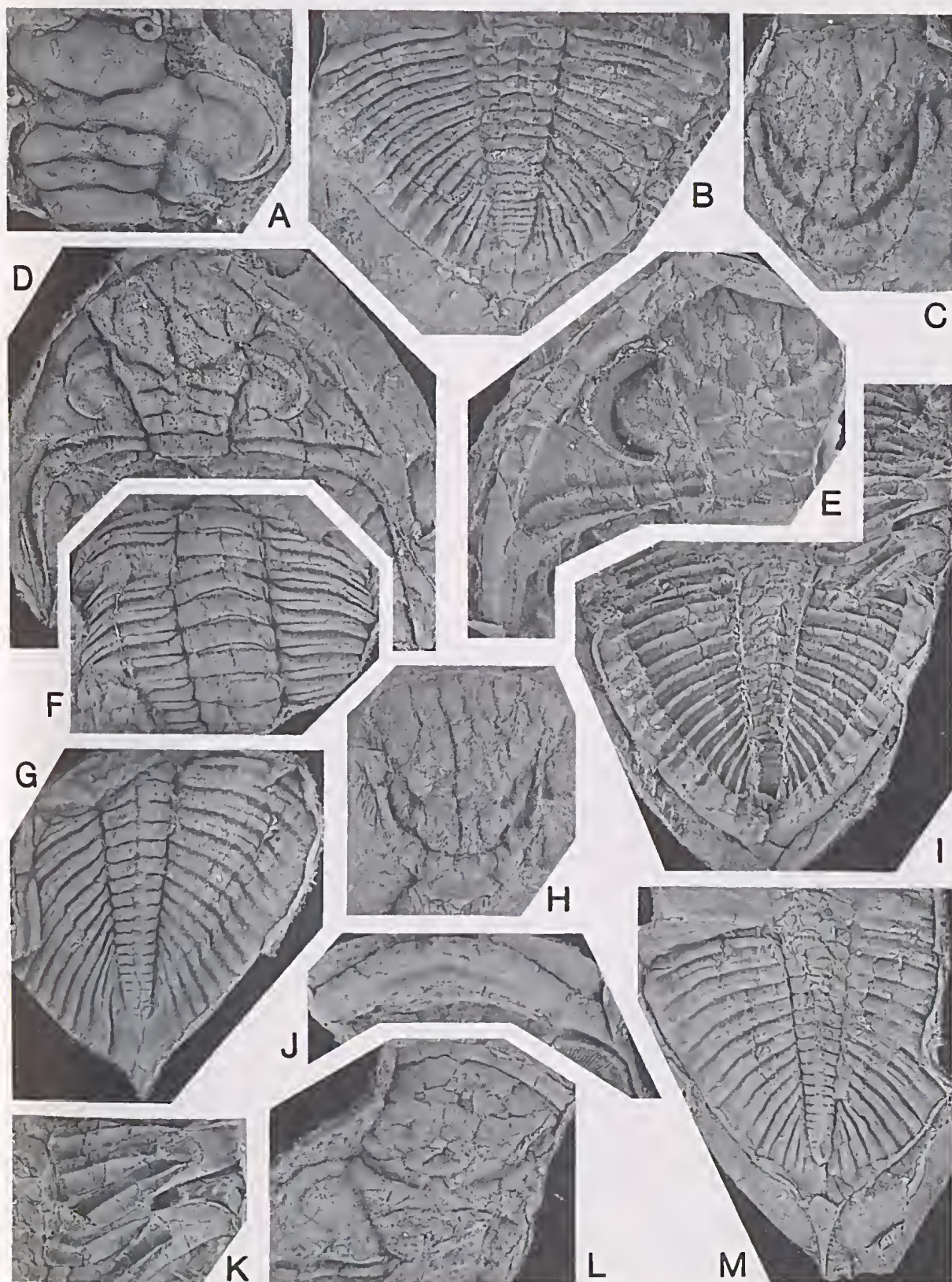
Granules on axis of thorax and pygidium are concentrated along posterior margins of rings and are virtually absent elsewhere. Abaxial part of pygidial pleurae and mucro are covered with a uniform granulation, but closer to pygidial axis and on thorax granules are present only along posterior edges of pleural bands. Doublure on pygidium and thoracic pleurae more densely granulated than dorsal exoskeleton.

REMARKS: Gill's description of *O. formosa* was based only on the holotype, but there are a number of characters that cannot be determined from that specimen because it is an internal mould and is also broken in places. For example, there is no information on surface sculpture, the shape of the anterior cephalic border, or the length and shape of the mucro, and the eyes are very poorly preserved. No other specimens of *O. formosa* with these features preserved are known from the type locality. Gill (1948) also illustrated as *O. formosa* an internal mould of a cephalon belonging to a much smaller individual than the holotype and coming from a different locality in the same formation and area. Numerous additional specimens from this locality are available in the National Museum of Victoria collections, and they include external moulds of cephalon and pygidia as well as articulated exoskeletons. They differ from the holotype in a few respects, mainly in having a

more weakly inflated glabella, less distinct furrows 1p and 2p, and eyes that extend much closer to the posterior border furrow. However, I attribute the differences to the very much smaller size of these specimens. The specimens from the Winneke Reservoir site, which are of intermediate size, fall within the range of variation in these features, and in all other features closely resemble the specimens from both of the Kinglake West localities.

Three other dalmanitid species have been recorded from the Late Silurian to Early Devonian of southeastern Australia, but each is in need of revision as the published illustrations and descriptions are inadequate. *Dalmanites wandongensis* Gill 1948 from the Dargile Formation (Ludlovian) near Wandong, Victoria, is based on a cephalon and an internal mould of a pygidium differing from *O. formosa* in that glabellar lobes 2p and 3p are not as inflated abaxially and the axial furrow is weaker; the 3p furrow is shallower; there is no eye platform; the lateral cephalic border is narrower and more convex (tr.); there is almost no change in slope from the frontal glabellar lobe to the anterior border; the front of the cephalon is deflected downwards medially in anterior view; and there are only 14 axial rings and 11 pleural furrows in the pygidium. *Odontochile meridianus* (Etheridge & Mitchell 1895) from the late Ludlovian-Gedinnian of the Yass Basin, New South Wales, is distinguished from *O. formosa* by its much smaller eyes that do not extend as close to the lateral border furrow; a narrower lateral cephalic border; a pygidium with 15-16 axial rings and 11-12 pleural furrows that are deflected more strongly backwards distally; anterior pleural bands on the pygidium that are weaker, particularly abaxially; and a mucro that is relatively narrower and more convex (tr.) at its base and is connected to the axial terminus by a strong postaxial ridge. The anterior cephalic border is not preserved in any of the types, but specimens of *O. meridianus* in the National Museum of Victoria collections show that it differs from the anterior border of *O. formosa* in contracting slightly in front of the lateral part of the frontal lobe and expanding medially to form a very short (sag.), broad projection. The types of *Odontochile loonesi* (Mitchell 1919), also from the late Ludlovian-Gedinnian of the Yass Basin, appear to be indistinguishable from *O. formosa* but there is no information on surface sculpture as the specimens are all internal moulds, and the only cephalon known lacks the anterior border. When more material of *loonesi* becomes available it may be necessary to place *formosa* in synonymy with that species.

Fig. 4—*Odontochile formosa* Gill 1948. All photographs except H are of latex casts. A, cranium NMVP82785, dorsal view, $\times 1.5$. B, pygidium NMVP82786, dorsal view, $\times 1$. C, hypostome NMVP 82787, ventral view, $\times 1.25$. D, cephalon NMVP82788, dorsal view, $\times 0.9$. E, cephalon NMVP82789, ventral view, $\times 1.3$. F, incomplete thorax NMVP82790, dorsal view, $\times 1$. G, pygidium NMVP82791, dorsal view, $\times 1$. H, internal mould of hypostome NMVP82792, ventral view, $\times 1.4$. I, K, M, pygidium and articulated thorax NMVP82793; I, M, ventral and dorsal views, $\times 0.9$; K, enlargement of pleural tips on posterior thoracic segments in ventral view, $\times 1.4$. J, L, incomplete cephalon NMVP82794 in ventral and dorsal views, $\times 1.25$.



Phylum ECHINODERMATA (P.A.J.)

Class HOMOIOSTEELEA

Order SOLUTA Jaekel 1901

Family RUTROCLYPEIDAE Gill & Caster 1960

Genus *Rutroclypeus* Withers 1933

TYPE SPECIES (by original designation): *Rutroclypeus junori* Withers 1933 from the Humevale Formation (Early Devonian) at Kinglake West, Victoria.

DIAGNOSIS: As given by Gill and Caster (1960) but the emphasis on flattened theca and proximal stele should be removed until proven.

REMARKS: The specimen described below may be used to argue that the proximal stele was not flattened as described by Gill and Caster (1960) and suggests other alternative interpretations for various parts of the stele. A closer correspondence with other solutan steles is interpreted (see Remarks on the species, below).

Rutroclypeus junori Withers 1933

Fig. 5, 6

1933 *Rutroclypeus junori* Withers, p. 18, pl. 5, figs 1, 2.1960 *Rutroclypeus junori* Withers; Gill & Caster, p. 30, pl. 1, figs 1-3, pl. 2, figs 2, 3.1967 *Rutroclypeus junori* Withers; Caster, p. S616.1982 *Rutroclypeus junori* Withers; Jell & Holloway, p. 42, fig. A.

HOLOTYPE: NMVP13681 from NMVPL229, Collins Quarry 2.4 km northwest of Kinglake West Post Office on the west bank of King Parrot Creek, Victoria. Humevale Formation—Early Devonian.

MATERIAL: One specimen, NMVP73811 from NMVPL 261

DIAGNOSIS (Gill & Caster 1960): "*Rutroclypeus* with spinose proximal stele having ten segments, the more distal of which may be deflected distally".

DESCRIPTION OF FIGURED SPECIMEN: The theca is round, 30 mm in diameter, consists of many polygonal plates reaching up to 4 mm in greatest dimension, and is preserved quite flat. Each plate has a short central spine. Around the thecal margin, plates curve back onto the other face very sharply and the median spine then appears to be marginal (as illustrated by Caster 1967, fig. 391-6). Marginal plates slightly dislodged on the right hand side (Fig. 5A) show the spines to be central with the marginal ridge linking the spines of contiguous plates.

The stele is relatively long (5.2 cm preserved) but is still incomplete. The proxistele consists of 10 circlets each of 4 plates arranged in four longitudinal series. Other longitudinal fractures of individual plates are irregular and when present may be near the axis or near

the outer margin and may be oblique, so they are clearly not following lines of weakness but were caused by compaction. The spines on the plates are much closer to the axis distally than they are near the theca, especially on the reverse side. The most proximal pair of obverse plates and the second and ninth plates in the lefthand obverse series lack spines. On the reverse the proximal pair of plates also lack spines. Between the centre line of the stele and the spine the posterior margin of each plate extends distally in a broad lobe beyond the more abaxial margin. On the obverse side there is no deflection of the distal plates.

Each plate in the proxistele has an anterior ledge on which the next anterior plate overlaps. Otherwise there is very little overlap of plates. The central suture on the reverse side becomes irregular to wavy distally with what appear to be small semicircular excavations (Fig. 5F, centre) in the plates of the last pair at their midlength. The mesistele consists of 1 plate on the obverse; the apparent sutures are fractures caused by compaction. On the right of the median stele (Fig. 5E, bottom right) is a spine that appears to be articulated. This suggests that all others on the proxistele may be articulated as well. On the reverse side the mesistele also appears to be a single plate as the fractures across it are highly irregular and due to compaction.

The distal stele (Figs 5D, 6) consists of an obverse and a reverse series of elongate plates that become progressively longer away from the theca. Transverse section of the distal stele is roughly diamond shaped with the margins of the reverse series apparently sitting just inside or against the margins of the obverse series. In lateral view plates of the obverse have an obtuse central elevation and their lowest point is at each end of the suture with the next plate in the series. Reverse plates that bridge the sutures between obverse plates apparently have a prominence to fit into the dip in the obverse lateral margin. All plates opposite the obtuse prominences have broadened lateral flanges upon which the obtuse prominences might fit but only the obverse plates are so situated in this specimen; reverse plates have all been displaced and lie inside the obverse series. Plates of the reverse series have a carinate median ridge, and are arranged so that there is one within the length of an obverse plate and that none of the junction sutures correspond to those of the obverse side. Consequently there are twice as many in the reverse series as in the obverse series. In the incomplete part of the distal stele preserved are 19 or 20 reverse plates but only nine and a half obverse plates.

An ornament of fine reticulate ridges, apparent on the proximal stele and thecal plates, is in broad terms radial away from the spine. On the distal stele the ornamentation is longitudinal, less reticulate and more granulate.

Fig. 5—*Rutroclypeus junori* Withers 1933, NMVP73811. All of latex casts. A, B, obverse and reverse, $\times 1.7$ and $\times 1.2$ respectively. C, D, lateral oblique view of distele showing plate arrangement, $\times 8$. E, obverse view of proxistele, $\times 5.5$. F, reverse view of proxistele—distele junction, $\times 11$. G, reverse view of proxistele, $\times 6$.

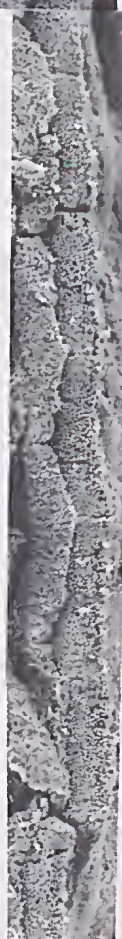




Fig. 6—Sketch of lateral view of plate arrangement in proximal part of distale of *Rutroclypeus junori*. Mesistele is enlarging plate at right. Obverse plates are upper series, reverse plates below. Drawn from Fig. 5D.

The arm is poorly preserved with only a single series of low wide brachial plates of the upper surface preserved. The inner side of the other series may be present beneath the upper series.

REMARKS: This specimen offers details on the thecal margin that uphold Caster's (1967) reinterpretation. Its greatest value is in the information it offers on the structure of the stele. The medial stele is seen to be formed by a single rather convex plate on each of the obverse and reverse sides. This in turn leads to the conclusion that the proximal stele had a subcircular or at least a transversely oval section and is flattened only by compaction. The common longitudinal fracture of plates is consistent with flattening an oval shape. Such a proximal stele is unlikely to have joined into a theca as flat as that suggested by Gill and Caster (1960, fig. 6) but such a section for the theca is not impossible. I cannot say what the thecal height was on available information. At the type locality of *Rutroclypeus junori* all other echinoderms with a sealed interior, including several with a considerable internal cavity such as blastoids, have been flattened without sediment filling the thecal cavity; plates have accommodated by fracture as in *Rutroclypeus* instead of by dislocation.

The structure of the distal stele is biserial and its cross-section is identical with that of *Dendrocystites sedgwicki* Barrande (see Caster 1967, fig. 372). Moreover the lateral view of the distal stele is very similar in these two genera in the way the plates fit together (Fig. 5D). This specimen and the recent note on *R. withersi* (Jell & Holloway 1982) suggest that a more detailed study of *Rutroclypeus* is warranted.

Class CRINOIDEA

Subclass CAMERATA

Order DIPLOBATHRIDA Moore & Laudon 1943

Suborder EUDIPLOBATHRIDA Ubaghs 1953

Superfamily DIMEROCRINITOIDEA Zittel 1879

Family DIMEROCRINITIDAE Zittel 1879

Dimerocrinitidae gen. et sp. nov.

Figs 7C-E, 8

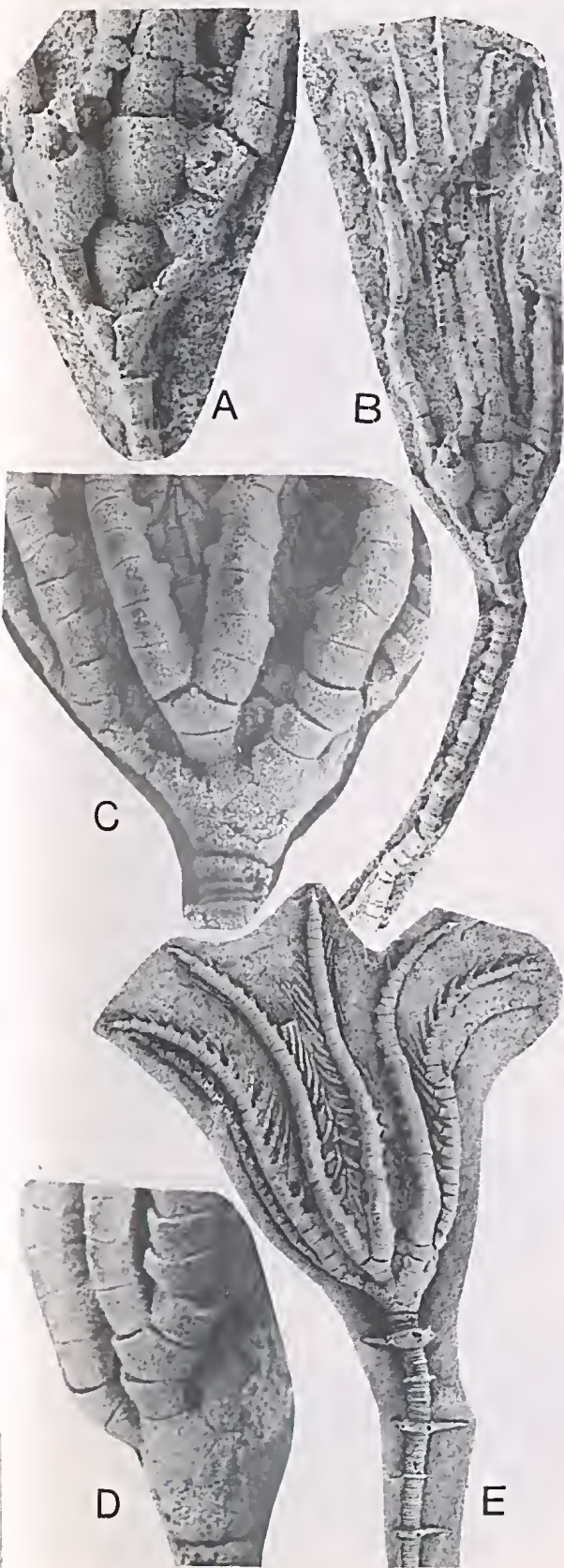
MATERIAL: One individual, NMVP74246, found in a block of rock removed from the floor of the dam site during preflooding quarry works. It was noticed as the material was being dumped elsewhere so its original location and horizon are unknown. The holotype of *Kootoonocrinus nutti* sp. nov. occurs on the same

block of rock but whereas both part and counterpart of that specimen are available the counterpart of the dimerocrinitid fell from the face of the block, presumably at the time of splitting.

DESCRIPTION: Cup small for family, low, conical; infrabasals 5, visible laterally but quite low; basals 5, hexagonal, approximately twice height of infrabasals; CD basal slightly enlarged; radials 5, in contact with each other laterally except in posterior interrady, with obtusely pointed lower margins; radial facet 0.8 of plate width, with broadly rounded outer margin, sloping out and down; primanal large, almost as large as CD basal upon which it sits, indirect contact with two posterior radials; further anal plates not known; interprimibrachs present but very deeply recessed between arms, one larger plate adjoining both first and second primibrach and supporting 2 smaller plates above. Arms dividing only once on primibrach 2 into 10 rami, uniserial, pinnulate, consisting of approximately 45 brachial plates per ramus; primibrachs fixed in theca; pinnules long, relatively stout, arising on alternate sides of consecutive brachials. Stem very slender, at least 25 cm long, circular in section, composed of cirriferous nodals separated by very low internodals varying from 3 to more than 20 per internode, and one or two non-cirriferous or weakly cirriferous nodals midway between the cirriferous ones or dividing the distance between strong nodals into three; distal part of stem with elongate irregular cirri apparently used in holding onto the substrate.

REMARKS: This specimen is assigned to the Camerata on the presence of interbrachial plates which are however not readily apparent. It is clear that these interbrachials are sutured to the sides of the brachial plates and that they are part of the tegmen, not simply fortuitously placed. Moreover, between the B and C rays may be seen the internal surface of a ramus from the opposite side of the theca (Fig. 7C, E) so that it would be very difficult for a long anal sac to be present without interfering with the mould of this ramus from the opposite side. On the other hand a short anal tube might not reach as high as the point where the opposite ramus appears or might be enveloped within the rami of the C and D rays. Such highly organised pinnulation is not known in inadunates of this age but is known in camerates.

As a dicyclic camerate with radial plates adjoining each other except in the posterior interrady it may be referred to the Dimerocrinitoidea. Without a bulged posterior, with infrabasals visible laterally and with relatively low basals and infrabasals it may be excluded from all the families except the Dimerocrinitidae. This specimen does appear relatively close to *Ptychocrinus* Wachsmuth & Springer 1885 with its low infrabasals, depressed interprimibrachials and uniserial arms but it differs from that genus in having far less obtrusive interprimibrachials, in lacking medial ray ridges and anal ridge, in the relative sizes of cup plates and in the structure of the stem. It is part of the uniserial *Ptychocrinus* stock that apparently continued from the Ordovician and Lower Silurian (Witzke & Strimple 1981, Bret 1978)



Ptychocrinus through the Silurian and into the Devonian with *Macarocrinus* Jaekel 1895. Consequently another group should be added to the three already proposed in this family (Witzke & Strimple 1981); the fourth group should include uniserial members of the Dimerocrinitidae namely *Ptychocrinus*, *Macarocrinus* and the new genus described above. Although it is clearly not assignable to any existing genus this specimen is left in open nomenclature until details of its posterior interray and a better preserved cup are available.

Subclass INADUNATA

Order CLADIDA Moore & Laudon 1943

Suborder CYATHOCRININA Bather 1899

Superfamily CYATHOCRINITOIDEA Bassler 1938

Family EUSPIROCRINIDAE Bather 1980

Genus *Kooptoonocrinus* nov.

ETYMOLOGY: From the Yarra aboriginal word *kooptoon* meaning one. It refers to the fact that both species of the genus are known from only one specimen.

TYPE SPECIES: *Kooptoonocrinus nutti* sp. nov.

OTHER SPECIES INCLUDED: *Kooptoonocrinus borealis* sp. nov. Its holotype is the specimen placed in *Ampheristocrinus typus* Hall 1879 by Springer (1926, pl. 31, fig. 1), from the Beech River Formation (Silurian) in Decatur County, Tennessee. It is housed in the National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A.

DIAGNOSIS: Cup conical with strong ray ridges; infrabasals 5; anal X in radial circlet, large, supporting 1 to 3 sac plates; radianal pentagonal, below and left of C radial; arms slender, primibrachs 3 or 5 axillary, branching isotomously 4 times to produce a characteristic branching pattern; stem transversely rounded, composed of short alternating nodals and internodals.

REMARKS: Springer (1926) referred the type of *Kooptoonocrinus borealis* to *Ampheristocrinus typus*, the type species of that genus, but whereas he stated that *Ampheristocrinus* was characterised by 3 infrabasals his own specimen is now known to have 5. Weller (1900) also considered the possession of only 3 infrabasals as a critical generic character. In view of the fact that important features of the arms and stem are not available from the type species of *Ampheristocrinus* I use the number of infrabasals to separate the new genus from *Ampheristocrinus*. Springer (1926) said he was uncertain of the number of infrabasals on his Tennessee specimen but Dr. P. M. Kier of the National Museum of Natural

Fig. 7—A, B, *Dendrocrinus saundersi* sp. nov. NMVP74239. All of latex casts. A, enlargement of theca in left posterior view, $\times 7$. B, left posterior view of latex cast of entire animal showing inner side of anterior arms, $\times 2$. C–E, Dimerocrinitidae gen. et sp. nov. NMVP74246. C, enlargement of theca and lower arms from left posterior, $\times 6$. D, posterior view of latex cast of theca, $\times 6$. E, upper stem and crown, $\times 3$.

History has recently determined that it has five infrabasals (written communication 17 June, 1982). It seems likely that Moore (1962) and Moore, Lane and Strimple (1978) used that specimen for their representation of 5 infrabasal plates in *Ampheristocrinus* also.

Although the family concept (Moore, Lane & Strimple 1978) appears to need some revision that is not attempted here. The new genus is assigned because it does not contradict the family concept and has some similarities with *Ampheristocrinus*. Its position in the phylogeny of the family is not clearly understood. *Kooptonocrinus borealis* sp. nov. is congeneric with the Australian specimen described below since they have the same thecal plate arrangement, narrow radial facets, branching pattern and stem structure. They may be distinguished by the Australian species having primibrach 5 (not 3) axillary and having the broad ridge running around its cup just beneath the radial facets.

Kooptonocrinus nutti sp. nov.

Figs 8, 9A-D

ETYMOLOGY: The species is named for Mr. Ron Nutt of Healesville who found and donated the only specimen. **MATERIAL:** Only the holotype, NMVP74245 is known. It was found in the same block of rock as the new dimerocrinitid crinoid described above. The block comes from the dam site but no more precise locality is known.

DIAGNOSIS: Infrabasals 5; one anal tube plate on top of anal X; strong ridge transversely on radial plates just beneath radial facets encircling theca; primibrachs 5 axillary; arms branching isotomously at six different levels but each branch divides only four times; stem of nodals and internodals near theca, ossicles becoming uniform in height distally.

DESCRIPTION: Cup conical with slightly attenuated lower part, approximately 5 mm high. Infrabasals 5, pentagonal when viewed laterally, 1 mm high \times 1.4 mm wide, with broadly obtuse central upper peak, ornamented with broad low but distinct ridges in "Y" form with 2 arms normal to the upper margins at their midpoints. Basals 5, hexagonal, 2 mm high \times 1.5 mm wide, ornament continuing from infrabasals and forming a narrow cross so that the four ends of ridges are normal to plate margins at midpoints of sides. Radials 5, pentagonal, with ornament of two ridges continuing from basals to outer edge of radial facet and a further ridge running transversely across the plate where the vertical ridges meet. The transverse ridges form a circlet around the cup at a level just beneath the midheight of the plates. Articular facets 0.6 of width of plate, horseshoe shaped, sloping outwards. Anal X plate large, situated in radial circlet, pentagonal with transverse upper margin, ornamented the same as radial plates except that a further ridge rises vertically from the central confluence of the ridges and continues onto the first tube plate. Radial not fully preserved but apparently pentagonal, below and left of C radial. Anal X supporting one large anal tube and possibly one or more very small

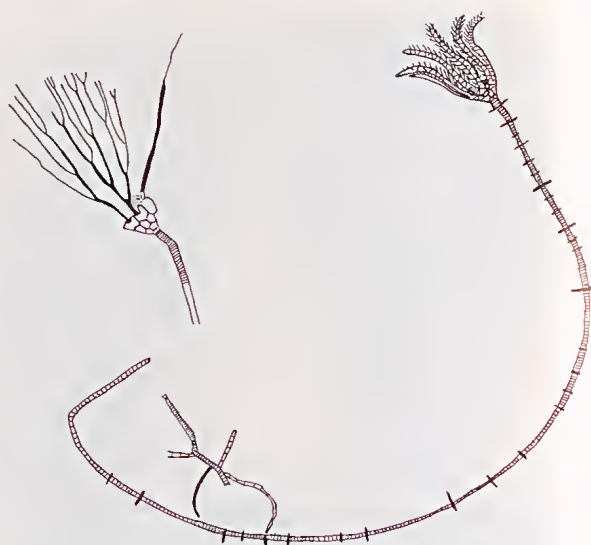


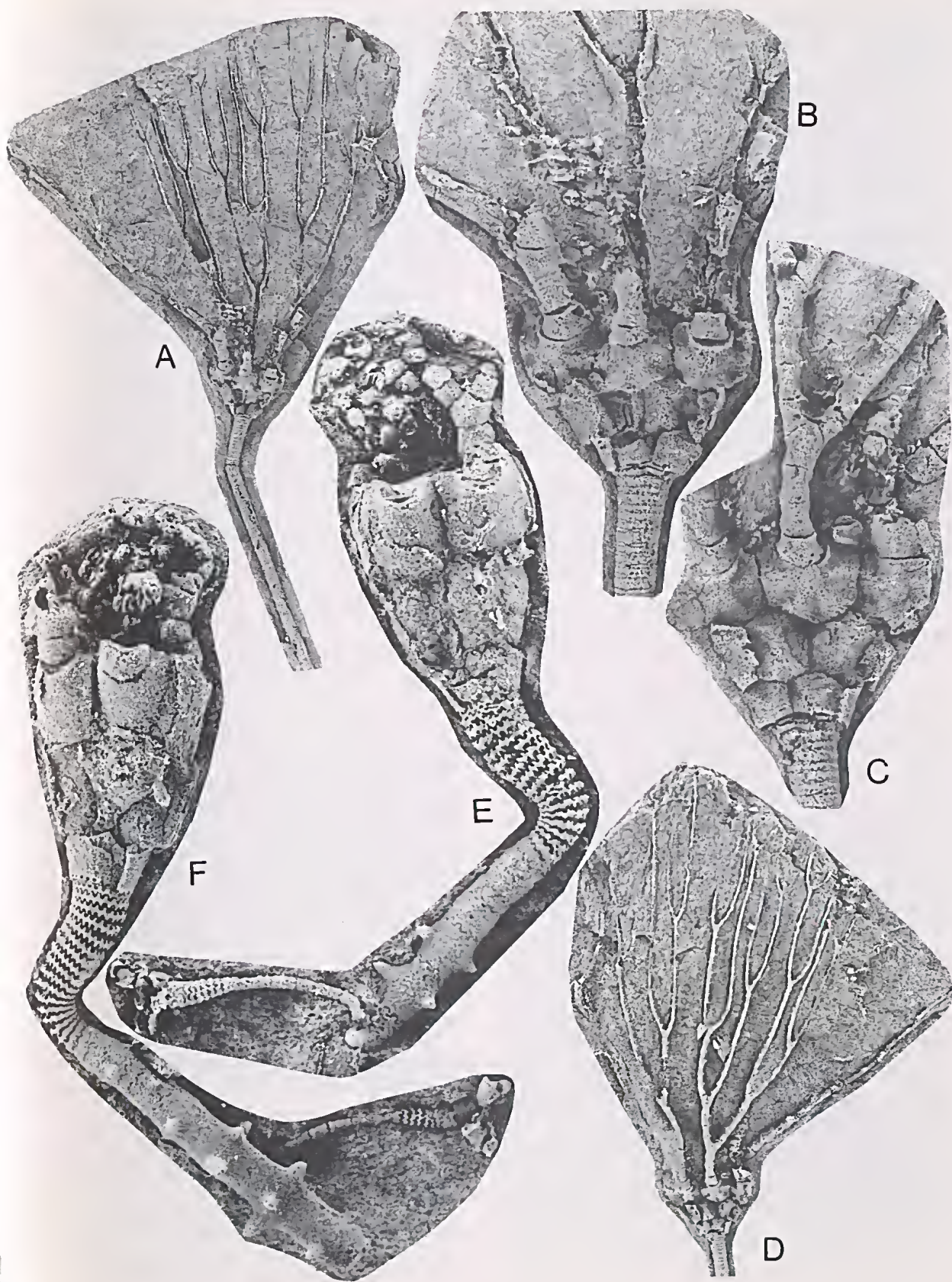
Fig. 8—Plan of slab with Dimerocrinitidae gen. et sp. nov. and *Kooptonocrinus nutti* sp. nov. showing length of stem and appendages.

plates beside the large one, remainder of anal tube not preserved.

Arms very slender, long, branching isotomously; primibrach 5 axillary; first primibrach shorter than others. Secundibrach 5 axillary; all 10 secondary divisions at same height above cup. Tertibrach 7 axillary on two outer branches of each arm; tertibrach 12 axillary on two inner branches; outermost branches of each arm with quaternary brachial 12 axillary and two central branches of each arm with quaternary brachial 12 axillary. Branching regular and consequently at six different levels above cup but no arm divides more than 4 times; branching pattern apparently identical in all arms. Deep food groove on inner side of brachials with small triangular covering plates. Tips of arms 30 to 35 mm above cup.

Stem circular in section, very long with 60 mm preserved and still incomplete; composed of alternating long and short nodals and internodals for proximal 10 mm but thereafter formed of ossicles of uniform height. **REMARKS:** Although thecal plates have been slightly dislodged so affording good illustration of plate margins in most cases, the anal interray is on the level of a bedding plane (on right of Fig. 9C) so that it has suffered maximum dislocation with anal X on one side of the mould and radial on the other dislodged and partially overriding the C radial. Moreover, the mould of the anal

Fig. 9—A-D, *Kooptonocrinus nutti* sp. nov. NMVP74245. All of latex casts. A, B, right lateral view and enlargement of thecal area of same, $\times 1.1$ and $\times 6$, respectively. C, D, left lateral view and enlargement of thecal area of same, $\times 1.4$ and $\times 6$, respectively. E, F, *Codiocrinus rarus* sp. nov. lateral views of latexes from part and counterpart of same individual, $\times 5$. Large individual NMVP73810 and small individual attached to its stem NMVP73812.



X and the few succeeding anal plates is imperfect so interpretation of the anal plate arrangement is not absolutely clear.

Superfamily CODIACRINOIDEA Bather 1890

Family CODIACRINIDAE Bather 1890

Subfamily CODIACRININAE Bather 1890

Genus *Codiocrinus* Schultze 1867

1867 *Codiocrinus* Schultze, p. 143.

1887 *Codiocrinus* Schultze; Wachsmuth & Springer, p. 152.

1967 *Codiocrinus* Schultze; Lane, p. 11.

1973 *Elicrinus* Prokop, p. 221.

1978 *Codiocrinus* Schultze; Moore, Lane & Strimple, p. T596.

1978 *Elicrinus* Prokop; Moore, Lane & Strimple, p. T606.

TYPE SPECIES (by original designation): *Codiocrinus granulatus* Schultze 1867 from the Eifelian of Germany near Prüm.

DIAGNOSIS: Cup high, conical, infrabasals 3 (or perhaps 5) visible in side view; 5 large basals and 5 large radials all symmetrical; no anal plates in cup; radials with narrow articular facets; arms branching dichotomously on primibrachs 3; stem with circular section and prominent crenularium.

DISCUSSION: Although the type species of *Codiocrinus* has not been redescribed or reviewed in detail since 1867 its features are well established. *Elicrinus* Prokop 1973 (type species—*E. procerus* Prokop 1973 from the Pragian Dvorce-Prokop Limestones of Czechoslovakia) is equally well known from Prokop's (1973) original description but it was referred to "Family *Incertae sedis*" by him. Since 1973 the collative review of crinoid families in the Treatise on Invertebrate Paleontology has made the search for an existing family to which *Elicrinus* might belong an easier task. Moore, Lane and Strimple (1978), however, referred *Elicrinus* to "Superfamily and Family UNCERTAIN". Within the Suborder Cyathocrinina *Codiocrinus* as defined above (i.e., as defined by Moore, Lane and Strimple 1978) will accept *Elicrinus* without any alteration to its diagnosis at all. In fact it is difficult to separate *C. granulatus* from *E. ornatus* Prokop 1973 which occurs in the Zlichov Limestone in Czechoslovakia except by the transverse ridge on the radial articulatory facet of the latter. Even the plate ornament of granules and ridges appears identical.

Species referred to *Codiocrinus* have been more globose than those referred to *Elicrinus* but *E. ornatus* begins to approach the globosity of *C. granulatus*. The slight variations in cup shape or in cup plate shape cannot be considered generically significant and the two genera should be considered synonymous. The species described below fits the generic concept in every respect.

Codiocrinus rarus sp. nov.

Fig. 9E, F

ETYMOLOGY: From the Latin *rarus* meaning rare.

MATERIAL: Only the holotype, NMVP73810, is known and it comes from NMVPL260.

DIAGNOSIS: Member of *Codiocrinus* with smooth calical plates; arms branching isotomously, uniserial non-pinnulate; three primary brachials per arm; stem with serrated outer margins to ossicles, with very short ossicles near cup, abruptly becoming higher away from cup and then with circlet of stout rootlets on each ossicle.

DESCRIPTION: Infrabasals 3, with serrated edge against top of stem, two large and 1 small plate, with obtuse angles at the base of sutures between basal plates, slightly outflared away from stem. Basals quadrangular, with curved lower margin, parallel lateral margins and almost straight upper margin but with broadly obtuse central peak. Radials quadrangular, with straight or slightly curved lower margin, straight lateral margins diverging slightly upwards, with semicircular excavation (i.e. radial facet) occupying approximately half plate width. Radial facet well rounded, sloping outwards, with transverse ridge, and fairly steep sides. First primary brachial completely filling radial facet and continuing outer face of cup. One other primary brachial of same size in each arm before primary axillary which has pentagonal outline viewed from exterior. All cup and arm plates are smooth and unornamented. Stem long, in two distinctly different parts. Proximal part consisting of 18 low ossicles having very strongly serrated sutures between them (i.e. each ossicle with strong crenularia), increasing only slightly in diameter towards cup, without rootlets. Distal part of stem consisting of high ossicles with strong crenularia and a circlet of five short stout spines on each. A few of the higher ossicles near the proximal end of the distal portion do not bear these spines. The distal end of the stem is not preserved.

DISCUSSION: *Codiocrinus rarus* may be distinguished from *C. procerus* (Prokop 1973), *C. ornatus* (Prokop 1973) and *C. granulatus* Schultze 1867 by its lack of granulate and ridge ornament on the cup and by differences in the size and shape of the radial facet. *C. schultzei* Follmann 1887 from the Early Devonian Hunsrück Shale of Germany has a more pronounced globose shape, is a larger form with thin plates and has wider radial facets than *C. rarus*.

The specimen is imperfectly preserved in two areas: 1, in the region of its basal plates which have collapsed inwards but those plates may be reconstructed from the margins of adjacent plates, and 2, in the region of the upper arms where it seems unlikely that there was further branching above the first dichotomy.

Suborder DENDROCRININA Bather 1899

Superfamily DENDROCRINOIDEA Wachsmuth & Springer

1886

Family DENDROCRINIDAE Wachsmuth & Springer 1886

Genus *Dendrocrinus* Hall 1852

TYPE SPECIES (by original designation): *Dendrocrinus longidactylus* Hall, 1852 from the Silurian Rochester Shale at Lockport, New York.

DIAGNOSIS: As given by Moore, Lane and Strimple (1978).

Dendrocrinus saundersi sp. nov.

Fig. 7A, B

ETYMOLOGY: This species is named for Mr. Rob Saunders of Melbourne Metropolitan Board of Works who collected the holotype and placed it in the Museum's collection.

MATERIAL: Only the holotype, NMVP74239 is known from beneath the right abutment of the dam.

DIAGNOSIS: Member of *Dendrocrinus* with high, relatively narrow radial plates, narrow horseshoe-shaped radial facets, unornamented thecal plates, anal sac high but relatively slim, anal plates smooth with lateral projections and an occasional spine, very slender arms branching isotomously 3 times and stem long, extremely small in diameter, and with beaded appearance due to irregular diameter and length of nodals.

DESCRIPTION: Crown elongate, narrowly cylindrical, more than 3 times as long as wide; cup relatively small, 6 mm high, conical with diameter less than height; infrabasals visible laterally, high, 0.25 of cup height (approximately), probably 3 in number (non availability of counterpart makes it impossible to count), pentagonal; basals 5 in number, hexagonal, 0.25 of cup height (approximately), centrally bulbous, descending to margin in gently sigmoidal slope; radials large, approximately 0.5 of cup height; C radial not as high as others and broadly quadrangular rather than pentagonal due to presence of radianal plate directly beneath it; anal X large, directly above CD basal from which it is separated by transverse suture, of irregular shape with 7 sides, 1 each against CD basal, C and D radials and radianal and 3 supporting three columns of anal plates; central column of large plates near anal X tapering distally over short distance; anal sac very slender, high (at least half height of arms), consisting of at least 8 columns of smooth quadrangular plates with prominent lateral projections that interlock with plates of adjacent columns; two lateral columns, supported by anal X, of plates of uniform size from base; radial articular facets half width of radial plate, sloping out and down, horseshoe shaped. Arms very narrow, with elongate oval section, branching isotomously three times (18 mm, 36 mm and 76 mm above radial plate on holotype), uniserial, primibrach 5 axillary. Stem very slender, circular in section, consisting of alternating nodals and very low internodals; nodals of variable height and diameter, producing a beaded appearance.

REMARKS ON HOLOTYPE: The counterpart of the holotype was not collected so the anterior of the cup is not available but the posterior provides sufficient information for specific identification. Plates of the cup have collapsed during burial but their outlines are still obvious although the precise shape and number of in-

frabasals plates remains doubtful. Due to the fact that moulds of arms pass into the rock away from the surface of the specimen (in particular ray D) it has proved impossible to obtain satisfactory latex casts of these structures. On withdrawal the latex is stretched beyond recovery or has not penetrated the mould at all. Different casts were obtained from successive applications of latex. The cast of the anal sac which runs up the centre of the specimen is of the posterior side which has collapsed in against the inner anterior side of the sac at the level of the first axillary plate. The inner anterior surface is visible a little further distally before the broken end of the mould of that structure. In this area, on the C ray side of the sac is visible a large spine normal to the plate surface.

REMARKS: As most of the species of *Dendrocrinus* are much in need of revision comparison of the species in hand has proved difficult. However it may be distinguished from all other species of the genus by a combination of its "beaded" stem, smooth thecal plates, slim anal sac and slim thrice-dividing arms.

Future review of the genus may reveal some subdivisions perhaps based on size of cup relative to arms coupled with size and number of columns of plates in anal sac. Until such a review is undertaken in North America *D. saundersi* may reside under this broad generic name.

Class OPHIUROIDEA Gray 1840

Order OEGOPHIURIDA Matsumoto 1915

Suborder LYSOPHIURINA Gregory 1896

Family ENCRINASTERIDAE Schuchert 1914

Subfamily ENCRINASTERINAE Schuchert 1914

Genus *Urosoma* Spencer 1930

Urosoma glabridiscus Talent 1965

Fig. 10A, B

1965 *Urosoma glabridiscus* Talent, p. 18, pl. 4, figs 4, 5, pl. 5, fig. 3, pl. 6, figs 2, 4, pl. 7, figs 1, 2, 5, 6, pl. 8, figs 3, 7, pl. 9, figs 2, 5.

HOLOTYPE: GSV 38103 from the Dargile Formation near Heathcote (Loc. 41, Parish of Heathcote, of Talent 1965), of Late Silurian age.

MATERIAL AVAILABLE: One external mould of the aboral surface, NMVP74243, and one external mould of the oral surface, NMVP74240, from beneath the right abutment of the dam.

DISCUSSION: These specimens agree with Talent's (1965) description of the species in every observable respect except that the Sugarloaf specimen has shorter ambulacra near the mouth frame than near midlength of arm, the arms taper strongly distally and the abradial margins of the ambulacra are weakly convex. The oral surface is not well enough preserved to see fine details of plates but the general organization is the same as in the Heathcote material. These specimens do not add

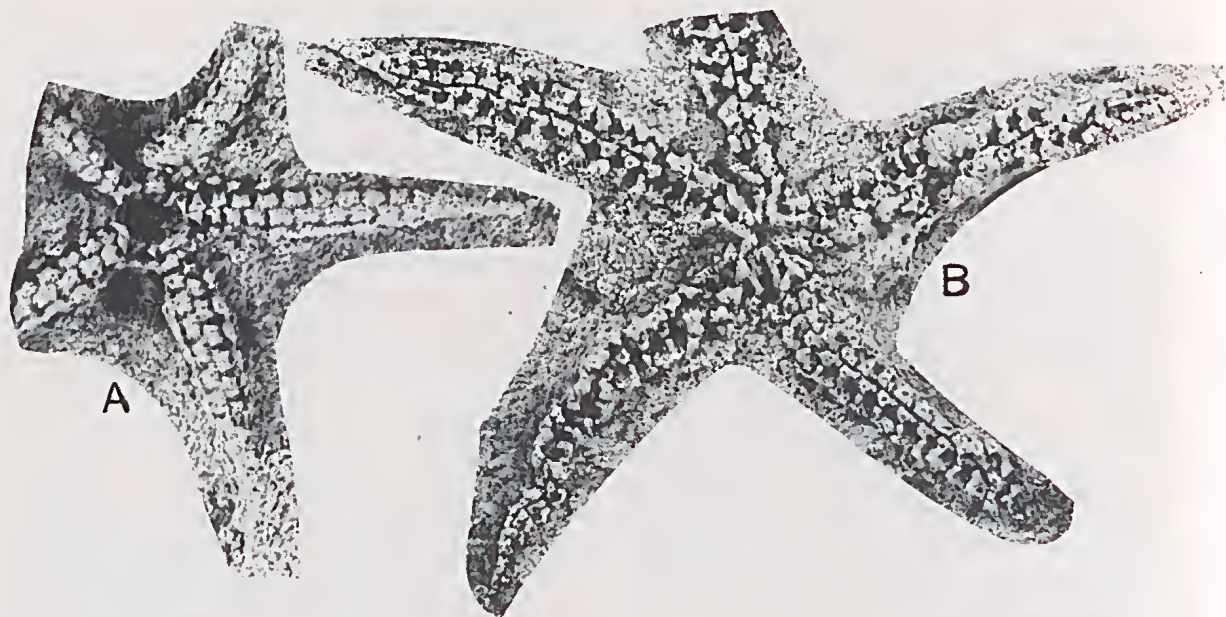


Fig. 10—*Urosoma glabridiscus* Talent 1965. A, aboral view of latex cast, NMVP74243, $\times 7$. B, C, oral views of latex cast of NMVP74240, $\times 4.5$ and $\times 7$, respectively.

anything to Talent's (1965) description and discussion of related taxa.

Subfamily ARMATHYRASTERINAE Harper & Morris 1978

Genus *Mausoleaster* nov.

ETYMOLOGY: From the Latin *mausoleum*, a term for a magnificent tomb that derived from that erected for Mausolus at Halicarnassus. It refers to the enormous mausoleum—the Sugarloaf Dam—built over this fossil

site. The suffix *aster* is Latin for star. Gender is masculine.

TYPE SPECIES: *Mausoleaster sugarloafensis* sp. nov.

DIAGNOSIS: Armathyrasterin without disc or marginal frame; with very heavy plates in mouth frame almost identical with those of *Lapworthura*; with very large podial basins on ambulacral plates; with pinnular adambulacral plates having large, possibly spinose adradial expansion; and with adambulacral plates only in contact adradially.

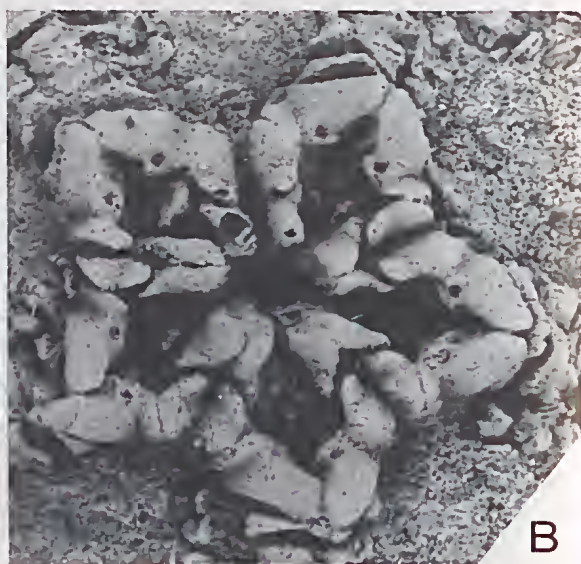


Fig. 11—*Mausoleaster sugarloafensis* sp. nov. NMVP74242. A, aboral view of latex cast, $\times 4$. B, enlargement of aboral view of mouth frame of same specimen, $\times 9$.

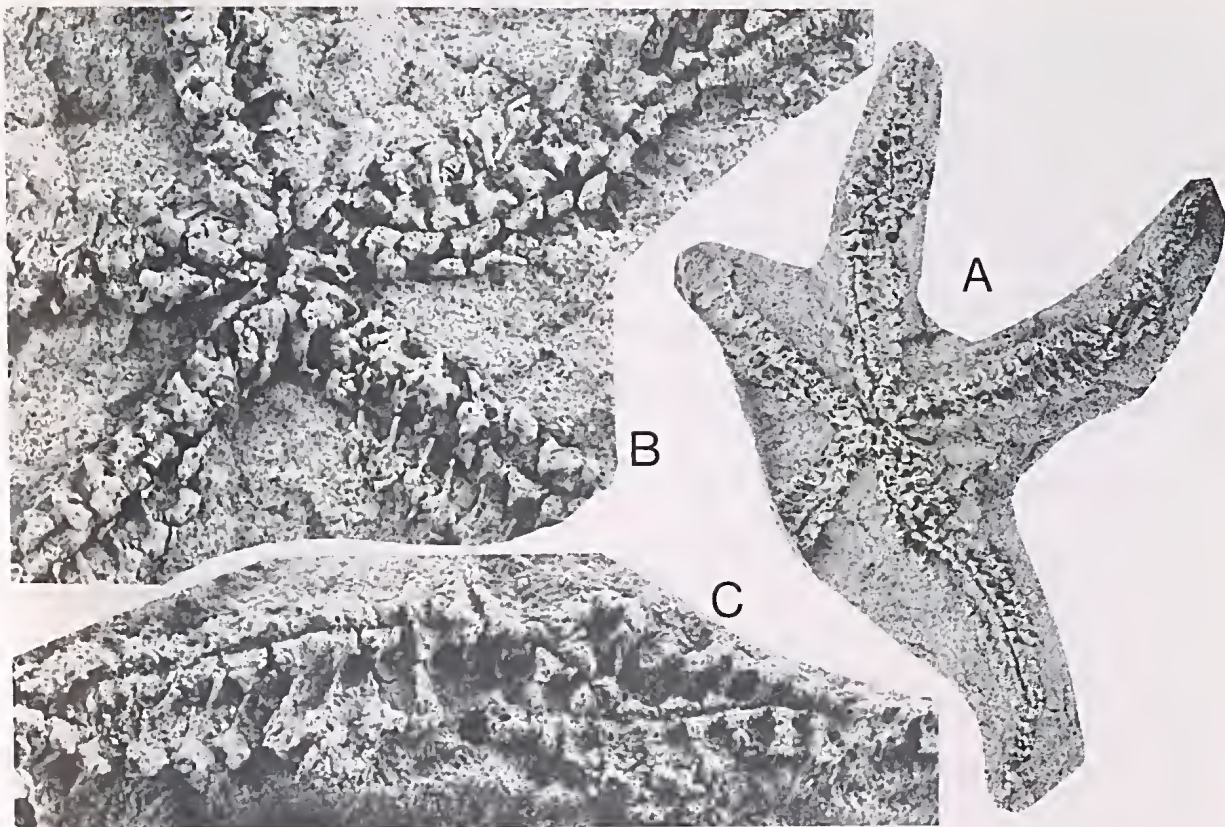


Fig. 12—*Mauleaster sugarloafensis* sp. nov. A, B, oral views of latex cast of NMVP74241, $\times 3$ and $\times 5$ respectively. C, enlargement of part of one arm of NMVP74241, $\times 7$.

DISCUSSION: The arm plates in *Mauleaster* are not as well preserved as in *Armathyra* Harper & Morris from the Upper Carboniferous of Pennsylvania, which is the only other genus of the subfamily, but there is sufficient detail to be certain of their structural alliance.

Harper and Morris (1978) suggested that *Armathyra* "appears to represent an end product of this (*Encrinaster*) lineage" but pinnular adambulacra in the Siluro-Devonian *Mauleaster* suggest the possibility of the two subfamilies existing as separate lineages from the Silurian to the Carboniferous. Moreover, the *Armathyra* could have been the primitive subfamily with its very large podial basins accommodated solely by the ambulacral plates and its pinnular adambulacra. The *Encrinaster* with reduced podial basins and more solid adambulacra appear more advanced and could have evolved from an early *armathyra*. With only the two genera of *armathyra* known it seems premature to speculate on their origin but at least a more logical alternative to that proposed by Harper and Morris (1978) now presents itself.

Mauleaster differs from *Armathyra* in the shape of the adradial part of the adambulacra, the much more robust mouth frame, lack of interradial disc and some minor differences in shape of ambulacra.

Mauleaster sugarloafensis sp. nov.

Figs 11, 12

MATERIAL: The holotype, NMVP74242 from NMVPL 260 is an external mould of the aboral surface. The paratype, NMVP74241 from beneath the right abutment of the dam, is an external mould of the oral surface.

DIAGNOSIS: As for genus.

DESCRIPTION: Five arms, evenly spaced; interradial disc absent.

Mouth frame 5-6 mm in diameter, consisting of large robust plates; first ambulacra much longer in the adradial direction than other ambulacra, becoming wider away from perradial line and crossed near the adradial end by a prominent furrow running obliquely out of the adradial line over two small pits (or apertures) and across the plate; first ambulacra and mouth angle plates abut along a flat face normal to long dimension of both plates; mouth angle plates project into pentagon formed by first ambulacra in pairs at midlength of each side, are crossed obliquely by a very deep furrow near their midlength, rise up steeply adaxial to this furrow and then finish with a high vertical flat face; adaxial ends of the mouth angle plates are almost as high as the distal ends of the first ambulacra which are the highest points

of the mouth frame. A much shallower broader furrow crosses the mouth angle plates, predominantly on their abradial and aboral sides, parallel to the deep furrow and halfway between it and the suture with the first ambulacral. In one interradius a very small elongate plate may represent an odontophore. On the oral side, mouth angle plates are elongate and blade like but with a slightly expanded, vertical, flat to weakly concave oral end. They are in contact at both ends but not in their middle section. No details of the plates of the mouth frame are available on the one specimen available.

Arms are rather wide, petaloid, up to 24 mm long and 4.5 mm wide on NMVP 74241; ambulacrals are not fused, are large, subquadrate, alternating with a weakly concave lateral margin, and supporting the large podial basins distally on the adradial side. Orally the ambulacrals are boot-shaped as is characteristic of the family; the podial basin is prominent on the posterior of the plate and a furrow runs across the plate from the basin. Many ambulacrals show oral or ventral processes at both proximal and distal ends. An adradial projection close to the proximal end of the ambulacral plate joins with a flat sutural junction onto the perradial end of the pinnular adambulacral; adradial plates expanded at their outer end into a large club-shaped structure that extends distally and touches the expanded end of the next adambulacral. This expansion has numerous projections and a vertical furrow at its midlength. Because of the disorientation of many adambulacrals the actual orientation of most of these processes is not clear. Some plate fragments adjacent to adambulacrals may be spines but they may also be dislodged pinnular fragments of the adambulacrals and lateral spines were probably not present. The pinnular part although very thin in dorsal or ventral view had some considerable height so that it was more a flat lath than a rod. The adambulacrals have twisted over onto the ambulacrals in several arms but have still retained the sutural contact so there must have been considerable flexibility in this junction. Distally on the arms where the pinnular part is very short no details are available.

ACKNOWLEDGEMENTS

We are grateful to a number of people for bringing material to our notice and/or donating it to the Museum collections. They include Ron Nutt of Healesville, Rodney Start, Dale Comrie of Christmas Hills, Darold Klindworth of the Yarra Valley Church of England Grammar School, Peter Lorenz, Betty Argo and Ray Saunders and Wayne Regan of the Melbourne Metropolitan Board of Works. We are also thankful to Prof. K. S. W. Campbell, A.N.U., for discussion of the material of *Reedops* and to Dr. P. M. Kier of the U.S. National Museum of Natural History, Smithsonian Institution for information on *Kooptoonocrinus borealis*.

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CERATODUS NARGUN, A NEW EARLY CRETACEOUS CERATODONT LUNGFISH FROM CAPE LEWIS, VICTORIA

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ABSTRACT: A new species of Early Cretaceous lungfish, *Ceratodus nargun*, is described, based on a lower tooth plate from Cape Lewis, Victoria. The tooth plate is unusually high, with simple punctations, radiating ridges and a narrow occlusal surface.

Cretaceous ceratodont tooth plates have been described from New South Wales (*Neoceratodus pattinsonae* (White 1926) and *Neoceratodus forsteri* (Kreff 1870)) and from Victoria (*Ceratodus wollastoni* Chapman 1914 and *Ceratodus avus* Woodward 1906). There are also records of skull elements and parts of the axial skeleton from Koonwarra, Victoria (Waldman 1971) and a scale from Gippsland, Victoria (Chapman 1912).

A tooth plate which does not fit the description of any known species has been found in Early Cretaceous (Aptian) deposits at Cape Lewis, Victoria. It is housed in the palaeontological collection of the National Museum of Victoria, Melbourne (prefix NMVP).

SYSTEMATICS

Order DIPNOI Muller 1844

Family CERATODONTIDAE Gill 1872

Genus *Ceratodus* Agassiz 1838

Ceratodus nargun sp. nov.

Fig. 1

DIAGNOSIS: Tooth plate high crowned and narrow with a straight lingual border and long narrow radiating ridges separated by deep wide clefts which reach the lingual edge of the toothplate; occlusal surface narrow and interrupted by the clefts between the ridges; ridge crests faceted; punctations simple round pits, randomly distributed; enameloid having growth lines; cusps persistent at the labial ends of the ridges and reaching to the top of the ridge crest; pulp cavity narrow and extending into each ridge.

TYPE SPECIMEN: NMVP157247, a left lower tooth plate.

TYPE LOCALITY: Shore platform at Point Lewis, Victoria (38°50'20"S, 143°34'46"E).

STRATIGRAPHICAL POSITION: Early Cretaceous, (Aptian) zone C of Otway Formation (Gleadow & Duddy 1981).

ETYMOLOGY: The species is named for the rock monster in aboriginal mythology.

DESCRIPTION: All of the characters listed in the diagnosis are present in the holotype, which can be identified as a left lower tooth plate by the supporting jaw bone.

The specimen is not complete as part of the first ridge is missing (Fig. 1). There are 4 other ridges, 2 almost complete. The posterior part of the tooth plate is well preserved. The tooth plate measures 4 mm across the occlusal surface in the broadest part behind the second ridge, and the longest ridge is 11 mm in length. The

tooth plate is about 18 mm long, and the breadth/length ratio is 0.20. Tooth material is 8 mm deep and the underlying bone 4 mm. Angles between the ridges are given in Table 1.

The lingual border is straight (Fig. 1A). Presence or absence of an inner angle is hard to determine as the anterior part of the tooth and bone is incomplete (Fig. 1A). However an inner angle is likely. The ridges radiate from a point. The crests of the ridges are faceted i.e., worn into an angular shape, with equal wear on the anterior and posterior faces (Fig. 1A). Clefts between the ridges are deep and wide and extend to the lingual edge of the tooth plate (Fig. 1A) effectively dividing the occlusal surface along its length. The ridges are 3 to 4 times as long as the width of the tooth plate. There is no posterior heel.

Enameloid with growth lines is present on the labial surface of the tooth plate. The growth lines are continuous with persistent laterally compressed cusps on the complete ridges (Fig. 1B). The broken anterior part and the damaged third ridge show that a narrow pulp cavity extending down each ridge was present (Fig. 1A, B). Punctations on the occlusal surface consist of simple round pits randomly arranged (Fig. 1A). The bone supporting the tooth plate has the loose trabecular structure typical of lungfish jaw bone. There is a shallow sulcus in the bone below the posterior part of the tooth plate.

REMARKS: NMVP157247 is very different from other Australian Cretaceous lungfish. *C. avus* from the Early Cretaceous of Victoria has tooth plates with parallel ridges and complex punctations (Woodward 1906). *C. wollastoni* tooth plates have radiating ridges and simple punctations, but the tooth plates have broad occlusal surfaces and thick ridges with rounded crests, even in small specimens (Chapman 1912). This is also true of *N. pattinsonae* (White 1926). The other ceratodont from the Cretaceous of Australia is *N. forsteri* (Kemp & Molnar 1981). This species has low-crowned tooth plates with radiating ridges and simple punctations, enameloid, growth lines and persistent cusps, but the occlusal surface is comparatively wide. *C. nargun* has an unusually high crowned tooth plate with a narrow occlusal surface divided up by wide deep clefts between the radiating ridges.

There are similarities with the Russian Triassic lungfish, *Ceratodus donensis donensis*, *C. donensis gracilis* and *C. multicristatus* (Vorobyeva & Minikh 1968). However, *C. nargun* has higher narrower tooth

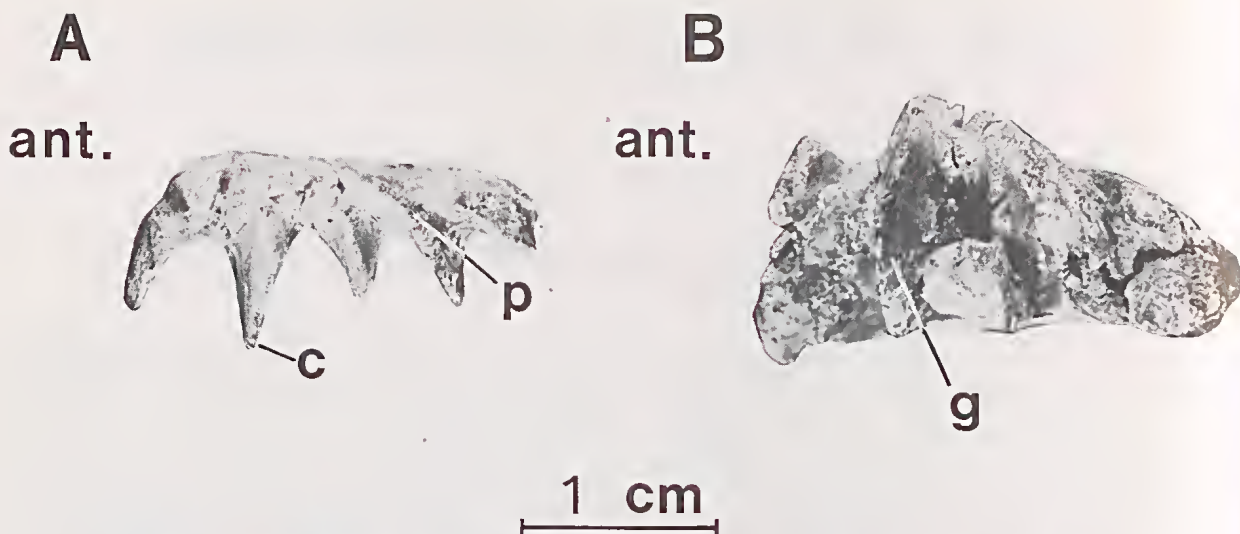


Fig. 1—*Ceratodus nargun* sp. nov., holotype NMVP157247. A, occlusal view showing cusps, straight lingual edge, narrow occlusal surface interrupted by deep wide clefts between the radiating ridges, faceted ridge crests, pulp cavity, absence of posterior heel and simple round punctations randomly arranged. B, labial view showing cusps, enameloid with growth lines, height of tooth and pulp cavity at the end of the third ridge. c.—cusps, g.—growth lines, and p.—pulp cavity.

plates with relatively shorter less strongly radiating ridges and comparatively shallower clefts and is therefore given separate specific status.

TABLE I
ANGLES BETWEEN THE SUCCESSIVE RIDGES OF THE TOOTH PLATE
OF *C. nargun*.

ridge	1-2	2-3	3-4	4-5	1-5
	13	21	20	27	82

ACKNOWLEDGEMENTS

I thank Mr. F. Bussat who found the specimen, Mr. Tim Flannery who prepared it and Dr. Tom Rich of the National Museum of Victoria who gave me permission to describe it. Dr. R. Molnar suggested the specific name.

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LATE TERTIARY MARINE TRANSGRESSION IN THE BRISBANE RANGES, VICTORIA

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ABSTRACT: The recent discovery of fragmentary marine fossils in the Moorabool Viaduct Sand in the Brisbane Ranges extends the area of known late Tertiary marine transgression of the Otway and Port Phillip Basins. A fossil shore platform exhibiting the ichnogenus *Trypanites* Magdefrau 1932, and rock borings attributed to *Pholadid* bivalves, is exposed in road cuttings on the Ballan-Geelong Road and provides further evidence of shallow marine conditions in this area in the late Tertiary.

For much of the Tertiary the Brisbane Ranges area appears to have been exposed, forming the hinterland to the marine basins. Its submergence in the Late Miocene-Early Pliocene was followed by marine regression and fluvial sedimentation in the Pliocene. The Moorabool Viaduct Sand was deposited during this transgressive-regressive episode. Local tectonics, coupled with eustatic sea level changes have influenced the distribution of Tertiary marine sedimentation in both the Brisbane Ranges and other areas surrounding Port Phillip Bay.

Extensive deposits of flat lying ferruginous sandstone and minor conglomerate form hill cappings in the Anakie, Steiglitz and Meredith areas to the west of Melbourne (Fig. 1). Similar ferruginous deposits outcrop east of the Rowsley Fault around the You Yangs, but are largely covered by Plio-Pleistocene basalts and alluvial sediments. The sediments are generally poorly exposed, but appear to be continuous with similar ferruginous deposits comprising parts of the Moorabool Viaduct Sand in the Geelong district (Fig. 1). They are therefore referred to the Moorabool Viaduct Sand. Most studies of Tertiary sediments in this area have concentrated on the marine sequences at Maude and to the south (e.g., Hall & Pritchard 1892, 1895, 1897, Doust 1968) although Harris & Thomas (1948) and Bowler (1963) briefly discussed the ferruginous sediments north of Maude.

The Tertiary sediments in these areas were deposited in the Otway and Port Phillip Basins on, and adjacent to, bedrock comprising Ordovician low grade metasediments and Upper Devonian granite. The area of Ordovician bedrock on the uplifted western side of the Rowsley Fault is here referred to as the Brisbane Ranges Block (Fig. 1). The purpose of this paper is to discuss the limits of marine transgression to the north of Maude during the late Tertiary, and to describe the angular unconformity between the Moorabool Viaduct Sand and Ordovician bedrock exposed near Anakie.

MOORABOOL VIADUCT SAND

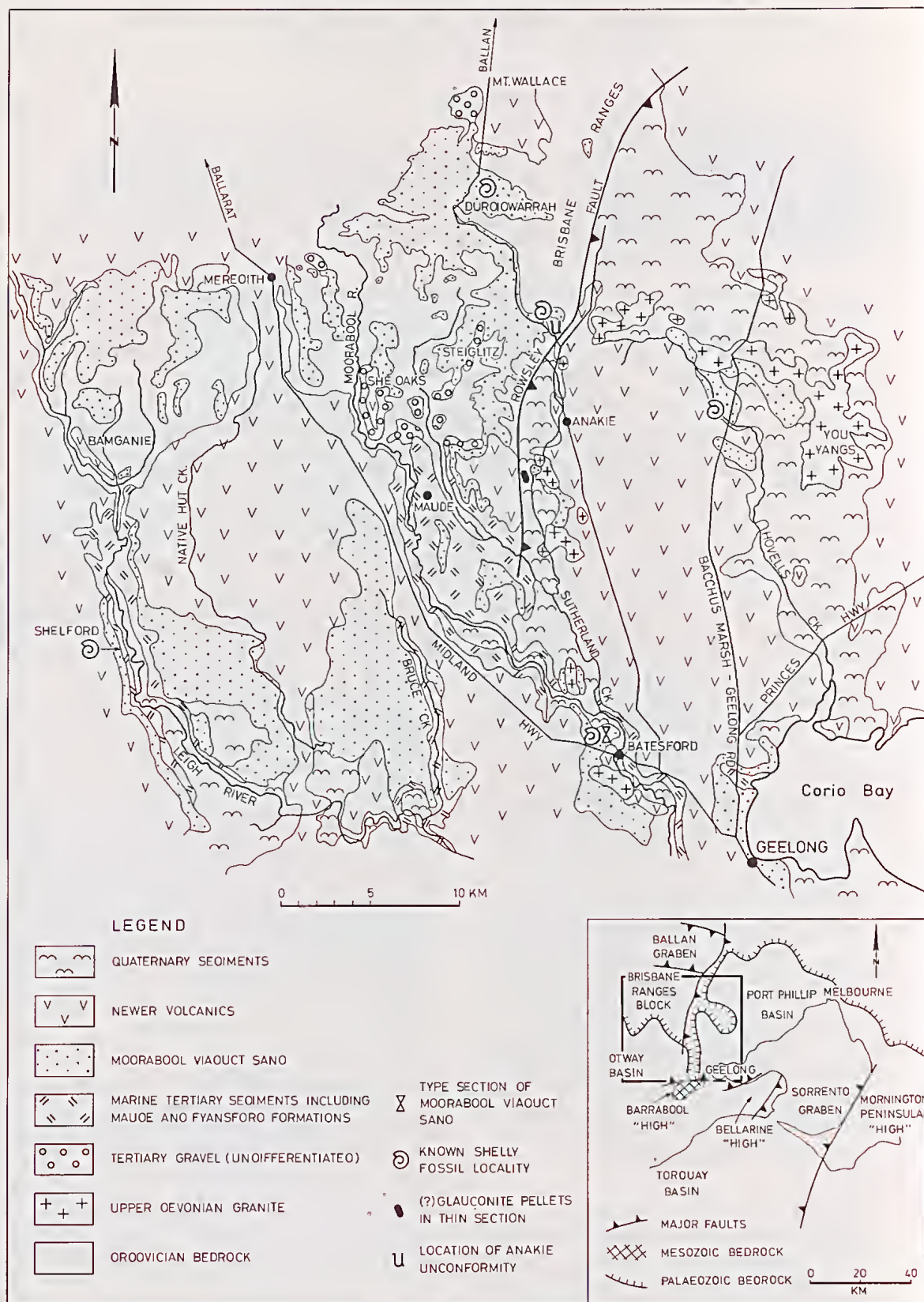
LITHOLOGY

At its type locality 2.5 km north of Batesford where the Geelong-Ballarat railway line crosses the Moorabool River (Fig. 1), the Moorabool Viaduct Sand comprises an upper sandy unit overlying iron-stained fossiliferous calcareous sand and sandy calcarenite. In the area north

of Maude, the calcareous facies is absent and the Moorabool Viaduct Sand consists mostly of moderately to well sorted, fine to coarse sand and sandstone with minor gravel and conglomerate. The sandstones are thinly bedded with planar bedding, rare graded bedding, small channels and planar and trough cross-stratification. The sediments are sometimes unconsolidated, but are usually strongly cemented by iron oxides. The sandstones consist of well rounded to angular common ("plutonic") quartz and minor feldspar, micas and heavy minerals. The angular quartz grains are usually intensely corroded by the ferruginous cement. The maximum exposed thickness in this area is 16 m along Sutherland Creek (east branch) where at one locality the sands contain well-rounded structureless ferruginous pellets of (?) oxidised glauconite. Fine to coarse grained gravel, rarely more than 3 m thick, occurs at the base of the Moorabool Viaduct Sand at some localities. The gravel contains subangular to very well rounded clasts of vein and common ("plutonic") quartz, slate, some sandstone and rare granite clasts. The gravelly beds grade vertically into the ferruginous sand and sandstone. Auriferous well rounded gravel occurs at the base of the Moorabool Viaduct Sand at Steiglitz.

PALAEONTOLOGY AND AGE

In the area north of Maude the fossils collected in the Moorabool Viaduct Sand are either fragmentary or too long ranging for an accurate age determination. Marine shelly fossils of late Tertiary age have been found near Durdidwarrah (Darragh in Makram & Neilson 1970, and pers. comm. 1977). Ferruginous moulds of gastropods, foraminifera and very rare bryozoans have been found in sand outcropping in the road cuttings on the Geelong-Ballan Road near Anakie, while gastropod fragments occur in sediments east of the Rowsley Fault near the You Yangs. Wood fragments were found at a number of



localities. Hall & Pritchard (1897) recorded leaf moulds and Doust (1968) recorded oyster shells and moulds of molluscs and leaves from localities to the south of Maude. Dennant and Mulder (1896) discovered marine shelly fossils in a ferruginous conglomerate at Shelford 20 km to the southwest of Maude. The fauna includes *Chlamys antiaustralis* and *Tylospira coronata* suggesting a Cheltenhamian (Late Miocene) age (Darragh *in* Abele *et al.* 1976). In the type area near Geelong, the Moorabool Viaduct Sand is of Late Miocene to Early Pliocene age (Darragh *in* Abele 1976). A similar age is inferred for the beds at Anakie and Durdidwarrah.

STRATIGRAPHIC RELATIONSHIPS

In the area south of Maude, the Moorabool Viaduct Sand disconformably overlies the marine, Middle Miocene Fyansford Formation: the disconformity is commonly marked by a phosphatic nodule band (Bowler 1963).

The Moorabool Viaduct Sand capping the hills north of Maude rests with marked angular unconformity on steeply dipping Lower to Middle Ordovician sandstone and slate. The unconformity exposed near Anakie is described below. Around the southern margins of the You Yangs, the Moorabool Viaduct Sand wedges against the You Yangs Granite and is locally enriched in feldspar and biotite derived from the granite.

At Sheoaks, Steiglitz, Meredith and near Mt Wallace, ferruginous sandstone and conglomerate referred to the Moorabool Viaduct Sand overlie fluvial gravel, sand, silt and clay. The fluvial deposits are considered to be of Tertiary age although they cannot be dated more accurately.

THE UNCONFORMITY AT ANAKIE

THE UNCONFORMITY SURFACE

The unconformity is exposed in two road cuttings 5 km north of Anakie on the Ballan-Geelong road. It is an irregular surface cut into a sequence of steeply dipping, tightly folded Ordovician slate and thin sandstones with occasional thicker sandstone beds, which are overlain with strongly angular unconformity by a basal conglomerate and fine to medium grained quartzose sands of the Late Miocene-Early Pliocene Moorabool Viaduct Sand. The unconformity is exposed over an east-west distance of 30 m, and has an observed maximum relief in the order of about 8 m in the western end of the cutting where there is a large gutter 8 m wide at the base, eroded into a thick sandstone interval forming the core of a tight anticline (Fig. 2). Small scale relief is typically in the form of small fissures or gutters, the formation of which has been controlled by preferential erosion along bedding, cleavage or fault planes.

THE MOORABOOL VIADUCT SAND

The lowermost deposit of the Moorabool Viaduct Sand upon the unconformity surface is a basal con-

glomerate, confined mainly to the large gutter, smaller gutters and depressions (Fig. 2). This is overlain by a dominantly fine to medium grained quartzose sandstone. The sandstone overlies and abuts the higher areas of the unconformity surface where the conglomerate was not deposited (Fig. 2).

THE BASAL CONGLOMERATE

The basal conglomerate consists of clasts of rounded to less commonly angular to subangular pebbles and cobbles of white vein quartz, rounded pebbles, cobbles and boulders of quartzite and quartz sandstone, rounded, weathered clasts of granite up to 85 cm maximum diameter, pebbles of ironstone containing angular grains of common ("plutonic") quartz, fresh feldspar and rare shelly impressions, and angular to subrounded slate clasts ranging from granule to large boulder grade. The matrix to the conglomerate is a medium to very coarse grained sand, with granule grade detritus to 0.5 cm, consisting of both white and clear quartz, feldspar, rounded platy slate fragments, and rare biotite, with a secondary whitish clay matrix. The granite clasts include an 85 cm maximum diameter medium grained leucogranite, consisting of quartz and feldspar with minor white mica and biotite, and a 70 cm maximum diameter coarse grained quartz-feldspar-biotite granite (with kaolinised phenocrysts of feldspar to 1 cm). The latter is associated with clasts of a much finer grained, less than 1 mm, aplitic phase speckled with fine biotite. The slate clasts range from platy, rounded sand and granule sized fragments up to more angular blocks about 0.5 m x 1.3 m. The largest slate blocks occur in the deep gutter cut into the Ordovician sandstone. On the western side of this gutter slate blocks can be observed strongly tilted but not quite broken off the palaeo-outcrop and subsequently buried by sands of the Moorabool Viaduct Sand. The larger slate clasts tend to lie with their maximum projection plane subparallel to the unconformity surface although small clasts are randomly oriented.

THE SANDSTONES

The sandstones overlying both the basal conglomerate and in places the unconformity surface are typically fine to medium grained, occasionally coarser grained, quartz arenites (*sensu* Okada 1971), which grade upwards from the basal conglomerate. Ferruginous moulds of benthonic foraminifera, especially miliolids, small gastropods and very rare bryozoans are contained in the sandstone unit. The sands exposed above the unconformity and in road cuttings to the west display low angle cross lamination and planar lamination. The sandstone occasionally contains scattered, typically rounded granule and pebble grade quartz, slate and occasionally granite clasts up to 30 cm. These larger clasts usually occur within the lower intervals of the sand where it overlies the basal conglomerate, or adjacent to higher areas of the unconformity surface against which the sand abuts. The finer clasts in places define a

Fig. 1—Geological Map of the Geelong-Meredith area (after Geological Survey of Victoria 1:250 000 Melbourne, Queenscliff, Colac, Ballarat maps).

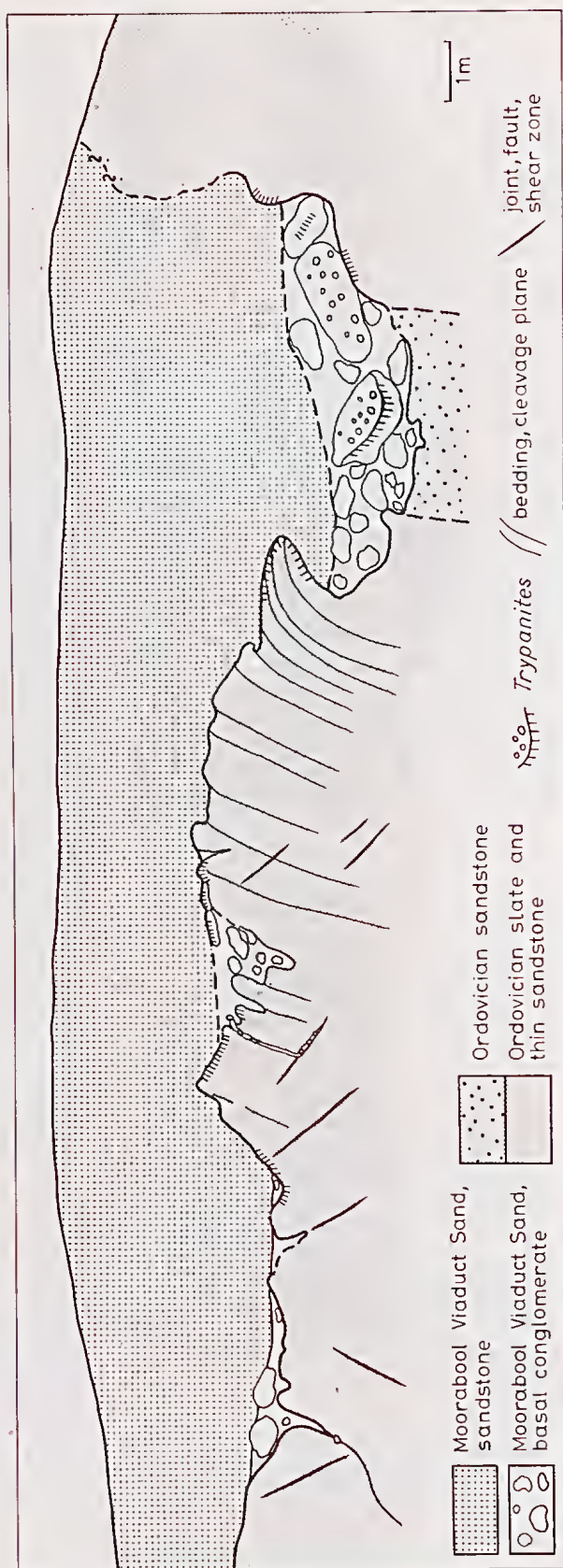


Fig. 2.—Detail of the unconformity exposed in the road cutting, Ballan-Geelong Road, Anakie, showing the basal conglomerate and sandstone of the Moorabool Viaduct Sand, *Trypanites* distribution and structural control of conglomerate distribution.



Fig. 3—*Trypanites* Magdefrau 1932: sectional view of borings exposed on the broken surface of a fragment of a slate clast from the basal conglomerate.

subhorizontal stratification, of granule-rich and granule-poor layers.

TRACE FOSSILS

Cylindrical holes may be observed in the slate of the unconformity surface and in the slate blocks of the basal conglomerate (Fig. 2). The holes are circular in transverse section, ranging in diameter from a few millimetres to 2 cm. In longitudinal section they are cylindrical to conical in shape, up to 4.5 cm deep, and with a hemispherical base (Fig. 3). No internal markings were observed, other than due to cutting the slaty cleavage, and fine pitting due to weathering of the slate. One hole was noted to have a small rim 2 mm high of cemented fine sand. The concentration of holes per unit area of rock is highly variable. They are commonly oriented perpendicular to the surface of the unconformity or the slate blocks but may be oblique. The latter orientation is more common in areas of higher density. With the burial of the unconformity surface and basal conglomerate by sands of the Moorabool Viaduct Formation many of the holes became infilled with sand. Some holes still contain their sand filling, while in one instance the slate has been weathered away to leave bulbous cemented sand casts of the holes on the base of the overlying sandstone.

The holes are considered to be borings, and are ascribed to the ichnogenus *Trypanites* Magdefrau 1932

(Bromley 1972). The borings in this instance are most probably due primarily to bivalves of the Family Pholadidae. The morphology of the borings compares closely with that described for present day pholadid borings by Evans (1970). Furthermore, they closely resemble pholadid borings figured by Evans (1970, pl. 7) and Warne (1970, pl. 2).

Most holes have been modified by abrasion subsequent to their formation. This modification has probably been accentuated by recent weathering. Abrasion has resulted in borings with a shorter longitudinal axis and a wider than normal opening. All that remains of some borings is the hemispherical base. Boring pholadids will avoid breaking into an adjacent boring, and will either divert or cease boring leaving a wall which may be as thin as 1 mm (Evans 1970). Abrasion has resulted in many of these walls in areas of close boring being worn away, producing a merging of holes. The abrasive effect of water and sediment on the borings has more than likely resulted in widening of holes, as well as the destruction of common walls, and the obliteration of any internal markings which may have been present. Abrasion may also have been responsible for the obliteration of finer, smaller borings and the modification of larger borings, so as to prevent recognition of the presence of other boring organisms, and assignment of some of the holes to organisms other than pholadid bivalves.

DISCUSSION AND INTERPRETATION OF THE UNCONFORMITY

The presence of borings attributed to pholadid bivalves and the occurrence of marine fossil fragments within the basal sands of the Moorabool Viaduct Formation indicate the existence of marine conditions, during deposition on the unconformity surface. The unconformity surface is interpreted as a wave-cut platform formed during the Late Miocene transgression. The large gutter eroded into the sandstone, and the smaller gutters eroded along bedding, cleavage or fault planes are considered to have been cut by preferential erosion along these zones of weakness by the action of breaking waves and backwash. As clasts accumulated within the depressions their to and fro movement by the wave and backwash action assisted in further erosion of the channels and gradual rounding of the clasts.

The basal conglomerate is a littoral-zone or strandline conglomerate deposited within depressions and channels cut into the wave cut platform. As is typical with such conglomerates, much of the detritus is of very local derivation. The slate clasts are obviously derived from the underlying Ordovician, while the vein quartz, quartzite and quartz sandstone clasts are almost certainly derived by erosion of the Ordovician bedrock. The large blocks of slate within the major gutter are considered to have been broken off the slate outcrop marginal to this gutter. In the slate outcrop on the western margin of the gutter there is a strongly tilted block of slate which was in the process of being loosened from the outcrop when burial by the Moorabool Viaduct Sand occurred. The granitic clasts are within the range of variation of the Devonian granites in the Anakie area outcropping east of the Rowsley Fault, and were probably derived from them.

As the transgression proceeded, it was probably followed close behind by the establishment of a rocky shoreline biota. This included at least pholadid bivalves, which inhabit the rocky substrate of intertidal and subtidal environments (Evans 1970). These organisms established habitats by boring into the unconformity surface and the slate blocks upon this surface. The occurrence of deeply abraded borings with partially or non-abraded borings indicate alternating periods of abrasion and boring activity. This is most probably due to periods of heavy wave activity, abrading the unconformity surface and slate blocks with finer gravel and sand, and probably also moving the larger slate blocks about within the gutter. During periods of more normal conditions the bivalves would re-establish their habitat, with new borings being formed amongst the earlier, abraded ones.

With time, the unconformity surface and basal conglomerate were buried by sand, and the rocky substrate biota displaced. The sands are well sorted, with horizontal and low angle cross-stratification typical of very near-shore and beach deposits (Clifton *et al.* 1971). The environment therefore remained at or very close to shoreline. Subsequently the transgression ceased and regression began, although it has not been possible to determine whether the highest beds in the outcrop at Anakie are transgressive or regressive sands.

SEDIMENTARY ENVIRONMENTS AND REGIONAL EXTENT OF MARINE TRANSGRESSION

The intense ferruginisation and poor exposure of the Moorabool Viaduct Sand throughout the area examined does not lend the unit to detailed facies analysis. Nevertheless both marine and non-marine facies are recognised locally. The inferred distribution of these facies, is shown in Fig. 4.

Calcareous marine facies have been described in the type area of the Moorabool Viaduct Sand in the Geelong district (Hall & Pritchard 1897, Singleton 1941, Bowler 1963, Doust 1968). All the ferruginous sediments north of Maude have previously been regarded as non-marine deposits (Harris & Thomas 1948, Bowler 1963). However the occurrence of marine shelly fossils at Durdidwarrah (Darragh *in* Makram & Neilson 1970 and pers. comm. 1977) indicates that the maximum marine transgression extended further north than was previously recognised. This is further supported by the occurrence of marine shelly fossils and a demonstrable fossil shoreplatform in the Durdidwarrah-Anakie area. Elsewhere recognition of marine facies is difficult.

East of Anakie probable marine strata abut the You Yangs Granite. Around the southern margin of the You Yangs near the Bacchus Marsh-Geelong Road, well sorted, planar-bedded medium to very coarse sands, locally containing well rounded frosted quartz grains, wedge against the granite. These deposits may be beach sands. Very rare gastropod moulds and ovoid limonitic pellets were found at one locality in this area, although it is not certain whether the gastropods are marine or non-marine forms. The limonitic pellets may be faecal pellets. Along Sutherland Creek (east branch) there are tabular and trough cross-stratified medium to coarse sands also containing abundant ferruginous pellets which may be oxidised glauconite or ovoid faecal pellets suggesting a possible marine origin for the sediments. These deposits are neither well sorted nor well rounded and may represent sand accumulation in offshore sand waves. The indirect evidence suggests that the beds exposed marginal to granitic outcrops east of the Rowsley Fault are probably shallow marine or shoreline sands deposited adjacent to and onlapping a granitic coastline which suffered erosion and provided detritus for the sands around the granitic coast and the conglomerate at Anakie.

In the southwest of the area, fossiliferous marine strata are recognised at Shelford. North of Shelford near Bamganie, the sediments are unfossiliferous and although they are texturally mature and contain ferruginous grains which may be oxidised glauconite pellets, there is no conclusive evidence for marine transgression in this area.

Fluvial facies in the Moorabool Viaduct Sand are recognised by the local occurrence of plant remains in sands and the presence of lenticular trough cross-bedded gravels. Ferruginous lenticular gravel deposits referred to the Moorabool Viaduct Sand overlie unconsolidated Tertiary fluvial deposits at a number of localities in the

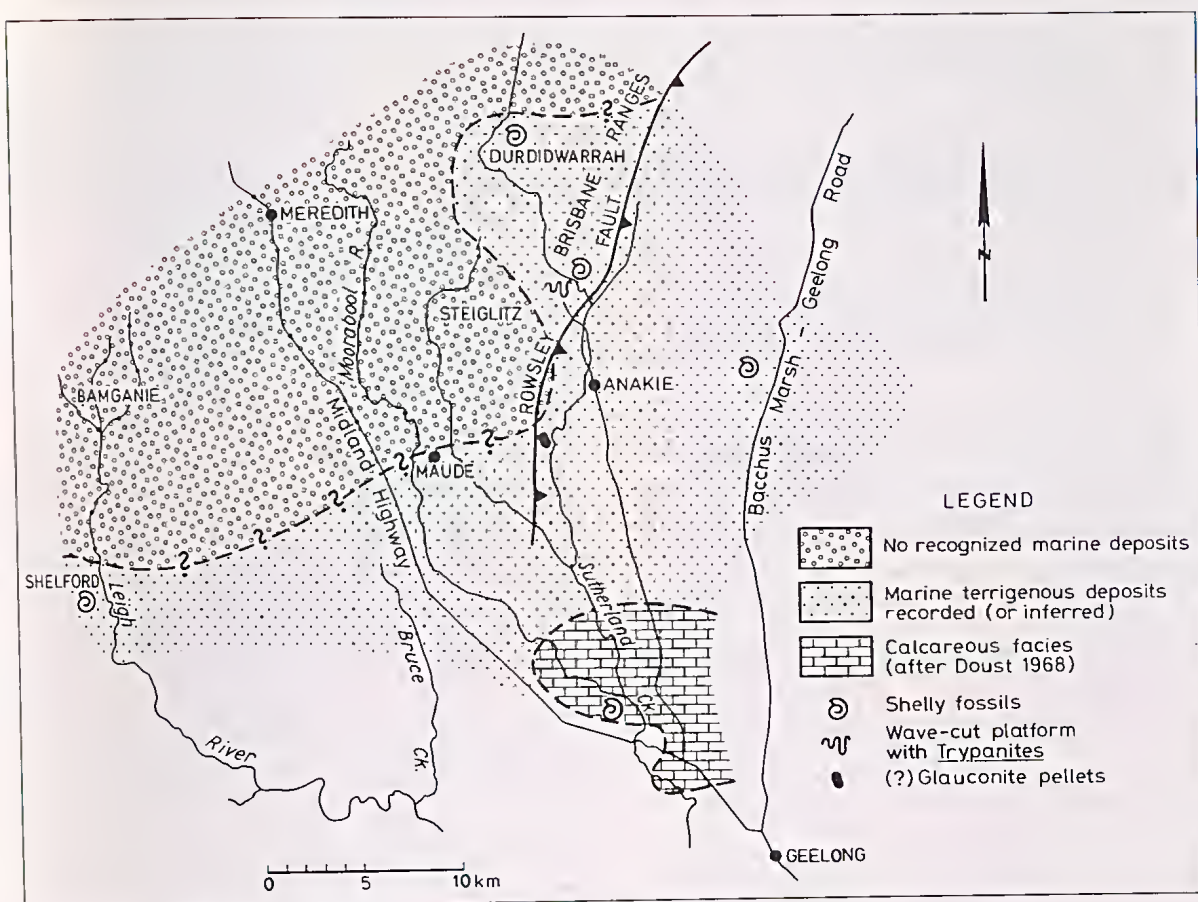


Fig. 4—Distribution of marine and non-marine facies of the Moorabool Viaduct Sand.

Mount Wallace, Meredith and Steiglitz areas and are overlain by both marine and non-marine ferruginous sands.

CONCLUSIONS

Throughout much of the Tertiary, the Brisbane Ranges Block was a topographically positive area forming the hinterland to the Otway and Port Phillip Basins (Fig. 1). Oligocene to Middle Miocene marine transgression in the Otway Basin extended as far north as Maude where shoreline deposits of the Maude and Fyansford Formations are exposed (Bowler 1963, Doust 1968, Bolger 1977). In other areas of relative uplift in the Port Phillip district (e.g., the Bellarine and Mornington Peninsula Highs), marine regression occurred in the Late Miocene (Holdgate 1976). Climatically induced Late Miocene marine regression caused shallowing of the sea in the Sorrento Graben, although sedimentation continued without a break (Mallett 1978).

In the Late Miocene-Early Pliocene shallow marine sedimentation continued in the Sorrento Graben (Holdgate 1976, Mallett 1978) while the Bellarine High (Bowler 1963) and the Brisbane Ranges Block underwent marine transgression. The transgression extended

as far north as Durdidwarrah on the Brisbane Ranges Block, eroding a rocky shore platform at Anakie and depositing the marine facies of the Moorabool Viaduct Sand. Marine transgression also occurred on the eastern side of Port Phillip Bay depositing the Black Rock Sandstone (Singleton 1941, Kenley 1967, VandenBerg 1973).

During later Pliocene times marine regression and fluvial sedimentation occurred on the "Highs" marginal to Port Phillip Bay, while shallow marine sedimentation continued in the Sorrento Graben (Holdgate 1976). Subsequent uplift along the Rowsley Fault has raised the Brisbane Ranges to their present elevation, and tilted the Newer Volcanics. In the east of Port Phillip the fluvial sediments are known as the Red Bluff Sand (Kenley 1967, VandenBerg 1973).

ACKNOWLEDGEMENTS

We wish to thank Dr C. Abele, Geological Survey of Victoria and Mr G. Holdgate, State Electricity Commission of Victoria for comments on the manuscript. The paper is published with the permission of the Director of the Geological Survey of Victoria. Figures were prepared by Mr G. Held, State Electricity Commission of Victoria.

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THE GENUS *BRACHIONUS* (ROTIFERA: BRACHIONIDAE) IN AUSTRALIA, WITH A DESCRIPTION OF A NEW SPECIES

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ABSTRACT: *Brachionus kostei* sp. nov. from waters of the Goulburn River, Victoria, is described and figured. It has affinities with the *B. urceolaris* group. Also described and figured is *B. forficula*, a new record for Australia. This Queensland species shown minor variations from the typical form. Twenty-two species and twenty-two subspecies/varieties of *Brachionus* from Australian waters are listed, with known distributions.

Although often the most abundant animals in Australian fresh waters, rotifers were neglected systematically and ecologically for almost 70 years following the work of Anderson, Shephard and others in the late 19th to early 20th century. With recent increased interest in freshwater ecology, and the recognition of the importance of rotifers in the trophic structure of Australian waters, there has been a proliferation of literature. In the last five years the number of recognised species has doubled, the known distribution of taxa hitherto recorded only from the Northern Hemisphere has been considerably extended, and endemic species in several families have been described (Sudzuki & Timms 1977, 1980; Shiel & Koste 1979, in press; Koste 1979, 1980a, b, 1981; Koste & Shiel 1980a, b, c, 1983; Green 1981; Shiel 1981 a, b; Walker 1981; Shiel, Walker & Williams 1982; Timms 1982; Brock & Shiel in press; Dussart *et al.* in press; Koste, Shiel & Brock in press; Tait, Shiel & Koste in press). In this paper, *Brachionus kostei* sp. nov. is described from Victorian waters, a local variant of *B. forficula* from Queensland is recorded for the first time from the continent, and the status of the cosmopolitan genus *Brachionus* in Australian inland waters is reviewed

SYSTEMATICS

Brachionus kostei sp. nov.

Figs 1, 2

TYPE MATERIAL: Eleven loricate females, sample number 865 Shiel collection.

HOLOTYPE: Loricated female, sample 865, collected 19 January 1982 by R. J. Shiel, Koste collection, genus *Brachionus* (11) No. 1.

PARATYPE: Numbers 2-3 (date and place of collection as for holotype) will be lodged in the South Australian Museum.

TYPE LOCALITY: Sheepwash billabong, adjacent to Goulburn Valley highway near Molesworth, Victoria at 145°31'20"E, 37°10'20"S.

DESCRIPTION: Pear-shaped lorica distinguished from other *Brachionus* forms (e.g., *B. urceolaris* or *B. leydigii rotundus*) through six strong pointed occipital and two characteristic foot-opening spines. Dorsal lateral and median apical spines relatively long, foot-opening spines somewhat convoluted (see Fig. 2b). Dorsal lorica (Fig.

1a) patterned with two unpaired median pentagonal facets, single triangular frontal panel below median spines, two lateral quadrangular-spherical panels. Pectoral or mental border of ventral lorica excised at margins rising to two blunt spines flanking medial U-shaped sinus (Fig. 1b). Striking ornamentation of ventral lorica behind this sinus: two cuticular ridges with granular borders run posteriorly, diverging slightly to lorica midpoint, ending in a panel enclosed by two large convex and three small concave arches.

MEASUREMENTS: Lorica length 108-140 μm , lorica width 110-115 μm , lorica height 55-65 μm , foot-opening ventral 22-25 μm , dorsal 12-15 μm .

ECOLOGY: The waters of Sheepwash billabong are of low conductivity (<50-200 $\mu\text{S cm}^{-1}$), magnesium bicarbonate dominated, commonly of pH 7.0-7.7, and of high transparency (<0.2-17 NTU), reflecting ground-water inflows from the relatively high water table, or from the nearby Goulburn River in times of flood (Shiel 1981). The assemblage with the new species comprised: abundant dinoflagellates (*Ceratium* sp.), monogonont Rotifera [*Ascomorpha saltans* Bartsch, *Asplanchna priodonta* Gosse, *A. herricki* De Guerne, *A. brightwelli* (Gosse), *Keratella tropica* (Apstein), *K. cochlearis* (Gosse), *Lecane bulla* (Gosse), *Polyarthra* cf. *vulgaris* Carlin and *Trichocerca similis* (Wierzejski)], Copepoda (*Boeckella minuta* Sars, *Tropocyclops Kiefer* n.sp.) and Cladocera (*Diaphanosoma unguiculatum* Guerne, *Daphnia carinata* King s.l., *D. lumholtzi* Sars, *Ceriodaphnia laticaudata* Muller and *C. cornuta* Sars). Co-occurrence of congeners in limnetic and littoral microfauna is typical of billabongs in this region (cf. Shiel 1976).

ETYMOLOGY: The species is named after Dr Walter Koste, Quakenbrück, West Germany, in recognition of more than 30 years dedication to rotifer systematics and ecology.

DISCUSSION: The new species belongs to the Formenkreis *urceolaris* (see Koste 1978, p. 76 and 1979, p. 239). It is characterised in particular by its conspicuously pointed spines, which are found in the following species groups: 1, *Brachionus nilsoni* Ahlstrom 1940 (cf. Ahlstrom 1940, Table 17: 1-5; 2, *Brachionus variabilis* (Hempel 1896); and 3, *Brachionus novaezealandia* (Morris 1913).

The first of these is constant in form, and is

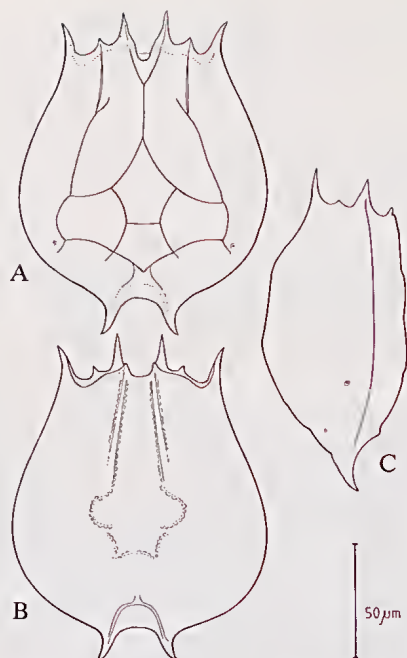


Fig. 1—*Brachionus kostei* sp. nov. A, lorica dorsal. B, lorica ventral. C, lorica lateral.

distinguished from the new species through short occipital spines, lack of median apical ventral spines and a ventral widely notched foot-opening (cf. Koste 1978). *B. variabilis* has very variable posterior spines. However, there is a constant and characteristic squamous projection over the foot-opening of the dorsal plate. This caudal process is absent in the new species (cf. Koste 1978, p. 80, fig. 9—5a-f). *Brachionus novaezealandia*, which shows many modifications, particularly in the construction of the submedian and lateral occipital spines and in the posterior spines (even within the same population), is always elongated in general form. Moreover, the median spines are always strikingly longer than the other apical spines. Facettation of the dorsal plate, or ornamentation of the ventral plate, is previously unknown (cf. Koste 1978, 1979).

***Brachionus forficula* Wierzejski 1891**

Fig. 3

DESCRIPTION: Morphology generally in accord with the description by Ahlstrom (1940). Characteristic four occipital spines, all sharply pointed. Two median spines slightly shorter flanking a V-shaped sinus. Mental margin excised laterally, undulate submedian sections with shallow medial depression (Fig. 3a). Stout posterior spines, subequal, pointed. Kneelike swelling on inner margin (cf. Fig. 3b) absent. Foot-opening ventral. Lorica lightly granulated.

MEASUREMENTS: Total length 208 μ m, width 93 μ m, anterior spines (median) 10 μ m, (lateral) 16 μ m, posterior spines (right) 82 μ m, (left) 90 μ m.



A



B

Fig. 2—*B. kostei* sp. nov. A, lorica ventral showing median sinus on mental margin and marked torsion of posterior spines. B, lorica dorsal.

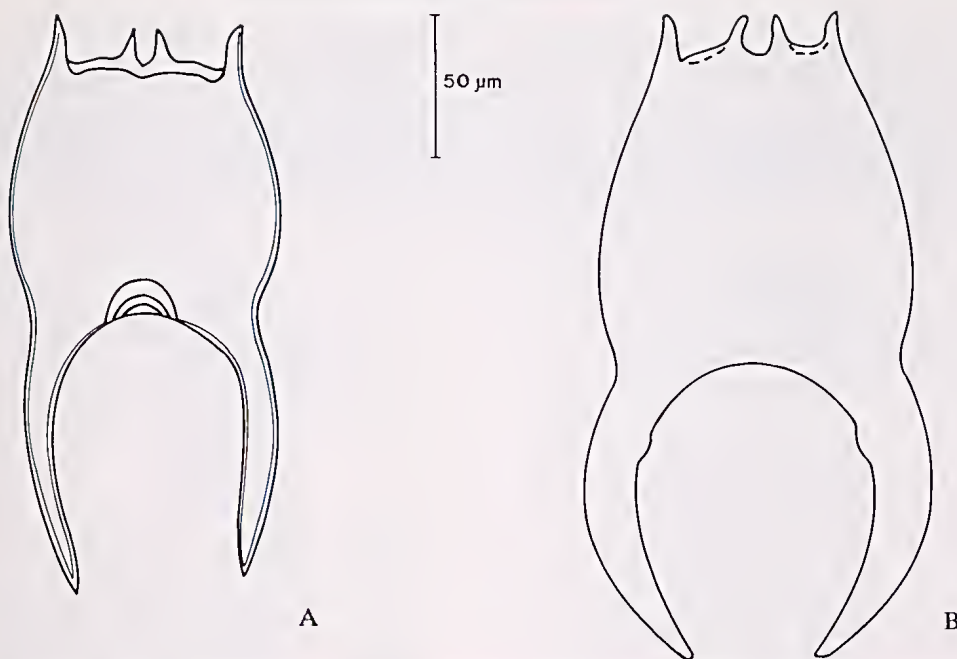


Fig. 3—*Brachionus forficula* Wierzejski A, ? ecotype from Queensland. B, typical adult form (redrawn after Koste 1978).

DISCUSSION: The variability of this species was described by Ahlstrom (1940), who noted that the swellings on the posterior spines may be absent on reduced forms. While the Queensland specimen resembles *B. forficula minor* Voronkov in this respect (see Kutikova 1970, figs 941a, b), it is in the upper third of the size range 106–256 μm reported by Ahlstrom. In the absence of further comparative material, the specimen is regarded here as an ecotype.

Characteristic of subtropical waters (Ahlstrom 1940), this rotifer has not previously been recorded from the continent. A single individual was recorded from a limnetic tow made by H. Midgely from Enoggera Creek Reservoir near Brisbane. It was forwarded by Dr. B. V. Timms, Avondale College, Cooranbong, N.S.W.

BRACHIONUS IN AUSTRALIA

In a review of the family Brachionidae, Pejler (1977) listed 13 species of *Brachionus* from Australian waters. Of these, *B. dimidiatus* (Bryce) was recorded from the New Hebrides (Russell 1957) and *B. zahniseri* Ahlstrom from New Zealand (Russell 1959). The remaining species were of wide distribution; no endemic taxa were recorded. *B. dichotomus* and *B. lyratus*, described by Shephard (1911) from Victoria, were omitted following Ahlstrom's (1940) revision of the genus, in which these species were regarded as probably synonymous with the widely distributed *B. falcatus* and *B. angularis* respectively.

With the descriptions of *B. baylyi* Sudzuki & Timms 1977, *B. keikoa* Koste 1979, *B. pinneanaus* Koste & Shiel in press, *B. kostei* sp. nov. and the rediscovery of *B. dichotomus* and *B. lyratus* (Koste & Shiel 1980 a, b,

1983; Sudzuki & Timms (1980) six endemic species are known from the continent. A further five new records and 22 subspecies or varieties, some of which apparently are endemic, were recorded in a study of the zooplankton of the Murray-Darling river system (Shiel, 1981a). All recognised taxa are listed in Table 1, with authority and known distribution.

The distributions in Table 1 represent only a small fraction of Australia's inland waters, and the list undoubtedly will be expanded with further investigations. The following trends are apparent: species recorded elsewhere as cosmopolitan also are pancontinental in Australia (e.g., *B. calyciflorus*, *B. angularis*, *B. plicatilis*). This group shows the greatest tolerance to variations in water quality, although, in accord with observations on the genus elsewhere, they are predominantly alkaline water species. *B. keikoa* is the only endemic species commonly found in alkaline waters, although *B. pinneanaus* is a rare component of alkaline waters in Western Australia (Koste *et al.* in press). The saline water species *B. plicatilis* shows some geographical variation, with the subspecies *colongulaciensis* confined to southeastern Australia (including Tasmania, at 42°S the southernmost record of the genus, cf. Pejler 1977), and the typical form across the continent (cf. Brock & Shiel in press, Koste *et al.* in press). *B. falcatus*, considered to be a cosmopolitan form, occurs throughout the Murray-Darling basin to 37°S. The remaining taxa are restricted to small geographical areas or single habitats, particularly billabongs. This group occupies neutral-acid waters, commonly of low conductivity, e.g., *B. urceolaris sericus* (pH 3.25) (Tait *et al.* in press). Notably, dwarf

TABLE 1
SPECIES OF *BRACHIONUS* RECORDED FROM AUSTRALIAN WATERS

Ssp and varieties are shown below each recognised species; * indicates apparently endemic taxa. A key to reference sources is given below. Predominant habitat is shown by R=river, L=lake/reservoir, B=billabong.

Key to sources: ¹Sudzuki & Timms 1977; ²Pejler 1977; ³Koste 1979; ⁴Shiel 1979; ⁵Shiel & Koste 1979; ⁶Koste & Shiel 1980a; ⁷b; ⁸c; ⁹Koste 1981; ¹⁰Green 1981; ¹¹Shiel, Walker & Williams 1982; ¹²Koste & Shiel 1983; ¹³Brock & Shiel in press; ¹⁴Koste, Shiel & Brock in press.

Taxon	Source	Distribution	Habitat
1. <i>B. angularis</i> Gosse	2	Cosmopolitan	R, L
<i>bidens</i> Plate	5	L. Mulwala, Vict.	
2. * <i>B. baylyi</i> Sudzuki & Timms	1	Myall Lakes, N.S.W.	
3. <i>B. bidentata</i> Anderson	2	Cosmopolitan	L
<i>testudinarius</i> Jakubski	5	E. Aust., N.T.	L, B
<i>jirovci</i> Bartos	5	R. Murray, S.A.	R
* <i>minor</i> Koste & Shiel	8	R. Murray, S.A.	R
4. <i>B. budapestinensis</i> (Daday)	4	Murray-Darling	R, B
5. <i>B. calyciflorus</i> Pallas	2	Cosmopolitan	R, L
<i>amphiceros</i> Ehrenberg	5, 13	Pancontinental	R, L
<i>aneuriformis</i> Brehm	5	E. Aust.	R, L
* <i>gigantea</i> Koste & Shiel	7	Menindee Lakes, N.S.W.	
6. <i>B. caudatus</i> Barrois & Daday	2	E. Aust.	R, L
<i>austrogenitus</i> Ahlstrom	11	lower R. Murray, S.A.	
<i>personatus</i> Ahlstrom	9	Magela Creek, N.T.	B
7. * <i>B. dichotomus</i> Shephard	6	E. Aust., N.T.	B
* <i>reductus</i> Koste & Shiel	6	E. Aust., N.T.	B
8. <i>B. dimidiatus</i> (Bryce)	8	Wodonga, Vict.	B
9. <i>B. diversicornis</i> (Daday)	4	E. Aust.	R, L
10. <i>B. falcatus</i> Zacharias	2	Pancontinental	R, L, B
* <i>reductus</i> Koste & Shiel	12	Magela Creek, N.T.	B
11. <i>B. forficula</i> Wierzejski	this paper	Tropical Qld.	L
12. * <i>B. keikoa</i> Koste	3	Darling Basin	R, B
13. * <i>B. kostei</i> n. sp.	this paper	Goulburn	R, B
14. <i>B. leydigii</i> Cohn	2	E. Aust.	B
<i>rotundus</i> (Rousselet)	5	R. Murray	B
15. * <i>B. lyratus</i> Shephard	8	E. Aust.	B
16. <i>B. novaezealandia</i> (Morris)	2	Cosmopolitan	R, L
17. <i>B. patulus</i> Muller	5, 10	E. Aust., N.T.	L, B
18. * <i>B. pinneanus</i> Koste & Shiel	14	S.W. W. Aust.	R
19. <i>B. plicatilis</i> Muller	2, 13	Cosmopolitan	saline L
* <i>colongulaciensis</i> Koste & Shiel	7	Vict., Tas.	saline L
20. <i>B. quadridentatus</i> Hermann	2, 10	Cosmopolitan	L, B
<i>melheni</i> Barrois & Daday	5	E. Aust.	L, B
<i>brevispinus</i> (Ehrenberg)	8	L. Boort, Vict.	
<i>cluniorbicularis</i> Skorikow	8	Wodonga, Vict.	B
*undescribed dwarf form	14	W.A., N.T.	B
21. <i>B. urceolaris</i> (Muller)	2	Cosmopolitan	
<i>bennini</i> (Leissling)	4	R. Murray	R, B
<i>nilsoni</i> (Ahlstrom)	5	R. Murray	R, B
<i>rubens</i> (Ehrenberg)	2	R. Murray	R, B
<i>sericus</i> (Rousselet)	12	N.T.	B
<i>sessilis</i> (Varga)	8	Wodonga, Vic.	B
22. <i>B. variabilis</i> (Hempel)	8	R. Murray	B

forms of several species (cf. Table 1) occur in these extreme biotopes.

There is no published ecological work on species' tolerances of Rotifera in Australian waters. However, there is some evidence that they counter the problems of living in billabongs (cf. Tait 1981, Koste & Shiel in press) by rapid generation times, the environmental cues for which may not be seasonal. Thus, the appearance of a species may be confined to weeks or days in appropriate

conditions, and large population densities (> 50 000 individuals l⁻¹) may be reached (Tait *et al.* in press).

Distinct habitat preferences or requirements produce species associations characteristic of each area, e.g., Alligator River billabongs have, in addition to cosmopolitan *Brachionus*, one or more of: *B. falcatus*, *B. dichotomus*, *B. caudatus personatus*, *B. urceolaris sericus* and *B. budapestinensis*. River Murray billabongs may have the cosmopolitan taxa, plus *B. quadriden-*

tatus, *B. bidentata*, *B. urceolaris* ssp. and *B. variabilis*, while the river proper may carry a mixed assemblage plus *B. calyciflorus*, *B. diversicornis* and (lower Murray only) *B. keikoa*. Western Australian waters, with higher salinities, commonly have only *B. calyciflorus* or *B. plicatilis* (cf. Brock & Shiel in press), although the work of Koste *et al.* (in press) suggests that ephemeral waters may carry rich rotifer communities.

ACKNOWLEDGEMENTS

Dr Walter Koste is thanked for verifying the new record from Victoria. Dr Brian Timms, Avondale College, Cooranbong, N.S.W. provided the material from Queensland, and Prof. C. H. Fernando, University of Waterloo, Ontario, brought this collection to my attention.

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SURVEY OF THE FISH FAUNA IN THE GRAMPIANS REGION, SOUTH-WESTERN VICTORIA

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ABSTRACT: The distributions of fishes in the Grampians Region of south-western Victoria were determined by a survey carried out between October and December 1979. Thirteen species, 7 native and 6 exotic, were recorded. Fish distributions were related to stream order and to habitat characteristics. Habitat preference of individual species appeared to be the most important factor determining distribution. Cluster analysis of sampling sites based on the presence or absence of fish species showed that broad habitat types did contain characteristic faunal assemblages. The effect of exotic species on the distributions of native fishes was unclear but circumstantial evidence suggested a fragmentation of the range of mountain galaxias, *Galaxias olidus* Gunther, by brown trout, *Salmo trutta* Linnaeus. The Grampians Region contained no single species or faunal assemblage not found elsewhere in Victoria. However, the eastern little galaxias, *Galaxiella pusilla* (Mack), was relatively common and the opportunity exists to preserve examples of the preferred habitat of this species.

The Grampians Region is one of the most important areas for wildlife in Western Victoria. It has been little altered by human settlement, primarily due to the steep and rocky nature of much of the terrain. During 1974 and 1975, the Fisheries and Wildlife Division, Victoria, conducted faunal surveys of the area (Emison *et al.* 1978). However, these surveys were concerned with terrestrial vertebrates and very few data were gathered on fishes. This paper presents the result of a survey of the fish fauna of the Grampians Region conducted between October and December 1979.

THE STUDY AREA

The area surveyed corresponds to region 2 of the four regions surveyed by Emison *et al.* (1978) and includes the whole of the Grampians Ranges together with the Black and Dundas Ranges, a total area of about 4530 km² of which about 48% is in public ownership (Fig. 1).

The ranges rise to an altitude of about 800 m and the elevated areas are steep and rocky with high runoffs. The low-lying areas consist of undulating deposits of sand with low runoffs and poorly defined water-courses due to seepage and evaporation loss. The average annual rainfall varies from 700 mm to more than 900 mm and average annual discharge from 560 ml/km², for MacKenzie River above Lake Wartook, to 48 ml/km² for the Wannon River above Dunkeld. Most discharge occurs during winter and spring.

The ranges are drained by the headwaters of the Glenelg, Wannon and Wimmera Rivers. The Glenelg River drains the western flanks and arises in the Victoria and Serra Ranges, initially following a northwesterly course through areas of swampland before turning southwesterly. It has one major storage in the study area, Rocklands Reservoir (built 1933, capacity 335 500 ML) and one small storage Moora Moora Reservoir (built 1933, capacity 62 900 ML). The Moora Moora channel, completed in 1930, allows water from the Glenelg to be directed into the Wimmera catchment.

The Wannon River drains the southern flanks of the ranges and follows a well-defined course only in its upper reaches, becoming increasingly swampy in the south and not normally flowing in summer. It has no major storages in the study area but a pipeline was installed in 1971 to direct winter flows from the headwaters northwards into Fyans Creek catchment. The Wannon and Glenelg Rivers meet to the southwest of the study area and the Glenelg continues until it enters the sea near the border between Victoria and South Australia.

The Wimmera River drains the northern and eastern flanks of the ranges and terminates at Lake Hindmarsh, 83 km north of the study area. Tributaries of the Wimmera River generally follow well-defined courses and two have major storages, Wartook Reservoir on MacKenzie River (built 1887, capacity 29 360 ML) and Bellfield Reservoir on Fyans Creek (built 1966, capacity 78 540 ML).

Areas of Crown Land contain a varied native flora, much of which remains in a relatively natural condition. Land has been cleared for agriculture in most areas outside Crown Land boundaries.

METHODS

Sampling was undertaken at 115 stations throughout the Grampians Region (Fig. 2) between 18 October and 17 December 1979 by electrofishing (82 stations), netting with a 1 mm diagonal stretch-mesh dip-net (37 stations, 8 of which were also sampled by electrofishing) and with 38 mm, 89 mm and 114 mm diagonal stretch-mesh gill nets (4 stations). Electrofishing was used to capture fish in easily-wadeable rivers. The length of river fished was normally 60 m (53 stations) although, where access was difficult, sampling was limited to 30 m (24 stations) and occasionally only isolated pools were sampled (5 stations). Dip-netting was used in slow-flowing backwaters and swamps where aquatic macrophytes were abundant. Gill nets were used in reservoirs and deep (>2 m) pools.

Fish were identified according to McDowall (1980c), and the length range (total length to nearest mm) and

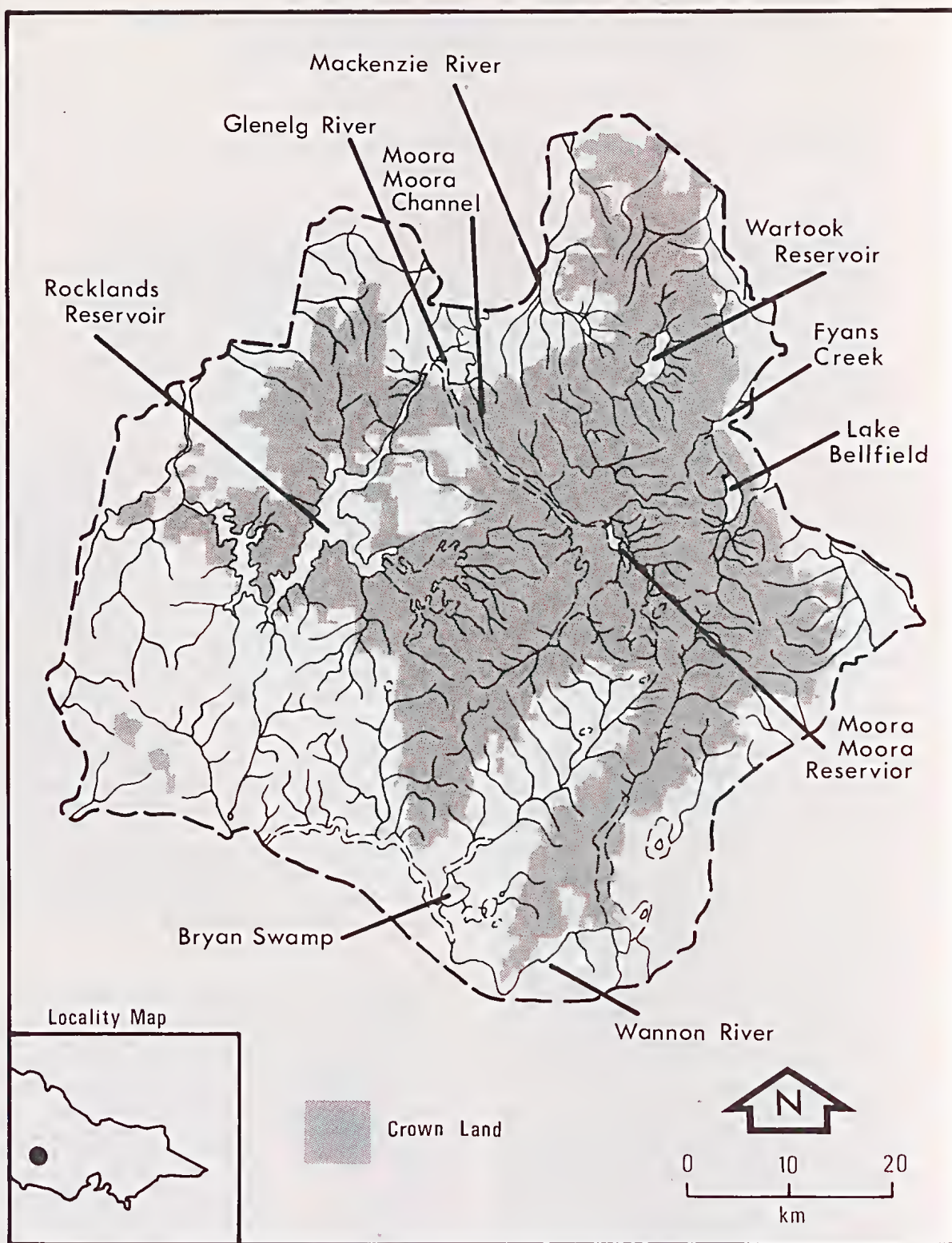


Fig. 1—Place names and areas of Crown Land in the Grampians Region.

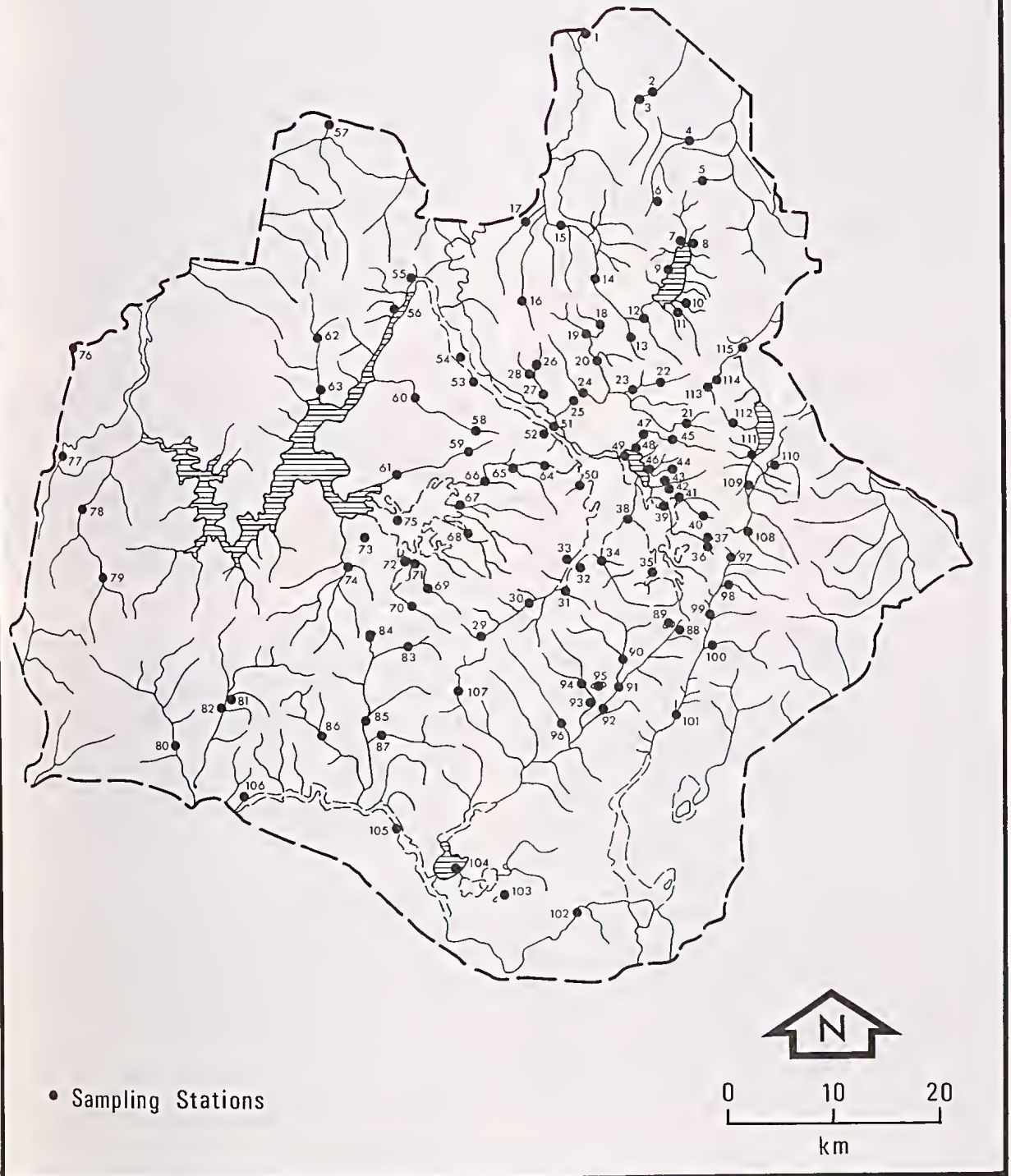


Fig. 2—Location of sampling stations in the Grampians Region.

TABLE 1
FISH SPECIES RECORDED FROM THE GRAMPIANS REGION
TOGETHER WITH THEIR LENGTH AND WEIGHT RANGES

Family	Scientific Name	Total Length range (mm)	Weight range (g)
NATIVE SPECIES			
Gadopsidae			
	<i>Gadopsis marmoratus</i> Richardson	29-270	0.5-104.5
Galaxiidae			
	<i>Galaxias olidus</i> Gunther	25-130	0.1- 18.9
	<i>Galaxiella pusilla</i> (Mack)	9- 37	<0.1- 0.8
Kuhliidae			
	<i>Nannoperca australis</i> Gunther	9- 75	<0.1- 6.2
	<i>Nannoperca obscura</i> (Klunzinger)	12- 33	<0.1- 0.6
Eleotridae			
	<i>Hypseleotris</i> sp. 4 (undescribed)	20- 55	0.1- 1.8
	<i>Philypnodon grandiceps</i> (Kreffit)	36- 77	0.4- 4.1
EXOTIC SPECIES			
Salmonidae			
	<i>Salmo trutta</i> Linnaeus	27-547	0.2-1864.5
	<i>Salmo gairdnerii</i> Richardson	321	428.8
Cyprinidae			
	<i>Carassius auratus</i> (Linnaeus)	11- 36	0.1- 0.8
	<i>Tinca tinca</i> (Linnaeus)	101-450	13.9- 925.0
Percidae			
	<i>Perca fluviatilis</i> Linnaeus	70-280	2.8- 326.0
Peociliidae			
	<i>Gambusia affinis</i> (Baird & Girard)	12- 33	0.1- 0.6

weight range (to the nearest 0.1 g) recorded for each species. Where identification was uncertain, specimens were preserved in 10% neutral formalin for later examination.

Following the style of Cadwallader (1979), for each station, the map reference, drainage system, approximate altitude, gradient and stream order (*sensu* Strahler 1957) were obtained from 1:100 000 topographical survey maps (Appendix). At each station the predominant substrate type and abundance of aquatic macrophytes were noted. Between 14 and 18 April 1980, some of the stations (Appendix) were re-visited to identify the more common species of aquatic macrophytes.

Cluster analysis was used to determine whether particular habitat types had characteristic faunal assemblages. Individual sampling sites were compared on the presence or absence of fish species using the flexible sorting method of Lance and Williams (1967) and the dissimilarity measure of Czekanowski (in Hellawell 1978). Sampling sites where no fish were captured were excluded from the analysis. The resultant clustering of sampling sites was represented graphically in the form of a dendrogram.

RESULTS

Fish were captured at all but 20 of the 115 stations. Thirteen species were recorded, 7 native to Australia and 6 exotic (Table 1). The freshwater blackfish, *Gadopsis marmoratus* Richardson, was the only native species to

attain a size in excess of 200 mm: the remainder were generally smaller than 100 mm. Of the exotic species, brown trout, *Salmo trutta* Linnaeus; rainbow trout, *Salmo gairdnerii* Richardson; tench, *Tinca tinca* (Linnaeus); and roach *Perca fluviatilis* Linnaeus, all exceeded 200 mm.

MOUNTAIN GALAXIAS

Mountain galaxias, *Galaxias olidus* Gunther, was the most widespread native species, occurring at 40 stations and in all three catchments (Fig. 3). The species was generally found in the high altitudes and steep gradients of first to third-order streams (Table 3), but was also recorded from the Moora Moora channel and Bryan Swamp. Most of these streams were flowing through undisturbed catchments (85% of stations) and were well-shaded by overhanging vegetation. Sand was the predominant substrate. Mountain galaxias was rarely associated with abundant aquatic macrophytes (Table 2).

BROWN TROUT

Occurring in both the Wimmera and Wannon systems, this species was recorded at 10 stations (Fig. 4). It was most commonly found in the higher altitudes and steeper gradients of the first to third-order streams and was present in Wartook Reservoir. Brown trout generally occurred (80% of stations) in streams flowing through undisturbed catchments, shaded by overhanging vegetation with little or no aquatic vegetation present. Brown trout occurred predominantly over a gravel substrate (Table 2).

FRESHWATER BLACKFISH

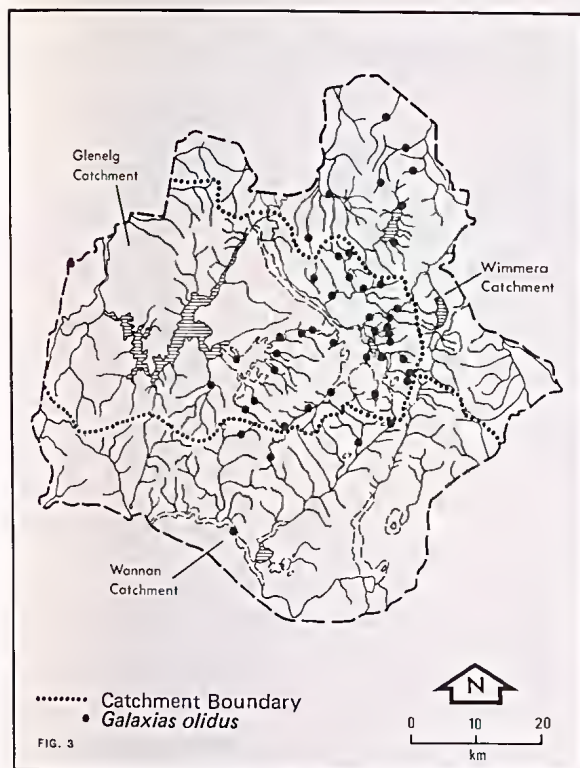
Freshwater blackfish occurred at 16 stations and in all three catchments (Fig. 5). It occurred at lower altitudes and in streams with gentler gradients than either mountain galaxias or brown trout. The species was most often found in streams flowing through undisturbed catchments and in slow-flowing stretches of water with abundant cover in the form of submerged logs, undercut banks and large boulders. Sand and gravel were the most common substrates (Table 2).

REDFIN

Occurring at 19 stations, this species was found in both the Glenelg and Wimmera catchments (Fig. 6). It occurred throughout second to fifth-order streams (Table 3) and was most common in backwaters and pools, particularly in the slow-flowing areas of the Glenelg River. The species was also present in Wartook and Moora Moora Reservoirs. Redfin occurred most frequently over a mud substrate and was often associated with aquatic macrophytes (Table 2); the most common species were the common millfoil, *Myriophyllum propinquum*, and an unidentified species of *Villarsia*.

FLATHEAD GUDGEON

Flathead gudgeon, *Philypnodon grandiceps* (Kreffit), occurred at 5 stations in the Glenelg and Wimmera catchments (Fig. 7). It was found in low-altitude, third and fourth-order streams (Table 3) and often (80% of stations) in areas where the catchment had been partially



Figs 3-6—Distribution of mountain galaxias, *Galaxias olidus* (3), brown trout, *Salmo gairdnerii*, and tench, *Tinca tinca* (4), freshwater blackfish, *Gadopsis marmoratus* (5), and redfin, *Perca fluviatilis* (6) in the Grampians Region. Boundaries (....) of the Glenelg, Wannon and Wimmera River catchments are shown.

TABLE 2
SUMMARY OF THE DISTRIBUTION OF FISH SPECIES IN RELATION TO ALTITUDE, THE GRADIENT, SUBSTRATE TYPE AND ABUNDANCE OF AQUATIC VEGETATION

Species	Altitude		Gradient		Substrate type	% of Stations with abundant aquatic veg.
	Mean (m)	Range (mm)	Mean (m/km)	Range (m/km)		
<i>Galaxias olidus</i>	287	150-600	27.5	0.0-200.0	S,(M),(B), (BD),(G)	29
<i>Salmo trutta</i>	374	220-560	35.0	0.0-133.3	G,(M),(BD),(B),(S)	20
<i>Gadopsis marmoratus</i>	264	150-440	11.1	0.9-128.6	S,G,(B),(M),(BD)	44
<i>Perca fluviatilis</i>	254	200-460	7.5	0.0- 28.6	M,(S),(G),(B)	50
<i>Phlypnodon grandiceps</i>	242	150-440	4.6	0.9- 12.5	M,(G),(S),(BD)	40
<i>Nannoperca australis</i>	228	200-280	1.9	0.0- 4.6	M,(S),(B),(G)	75
<i>Gambusia affinis</i>	202	150-220	1.8	0.4- 5.4	M,(S)	58
<i>Hypseleotris</i> sp. 4	232	200-260	1.5	0.0- 3.7	M	100
<i>Galaxiella pusilla</i>	233	180-240	1.4	0.0- 3.8	M,(S)	87
<i>Carassius auratus</i>	205	180-220	1.3	0.0- 2.5	M,(S)	50
<i>Tinca tinca</i>	268	220-440	0.8	0.0- 3.4	M,(S)	60
<i>Nannoperca obscura</i>	220		0.0		M	100
<i>Salmo gairdnerii</i>	440		0.0		M	0

G, gravel; B, boulders; BD, bedrock; S, sand; M, mud.

Parentheses indicate substrate also present but not abundant.

cleared for agriculture. The species was most often associated with slow-flowing stretches of river and a mud substrate. Common species of aquatic macrophytes included millfoil and floating pondweed, *Potamogeton tricarlinatus*.

SOUTHERN PIGMY PERCH

Southern pigmy perch, *Nannoperca australis* (Günther), was positively identified at 20 stations and occurred in all three catchments (Fig. 8). The open circles in Fig. 8 represent stations where southern pigmy perch was provisionally identified in the field but no specimens were taken. When these sites were revisited between 14 and 18 April 1980 they no longer contained water.

Southern pigmy perch was generally associated with pools and quiet backwaters found in low-lying streams and swamps and in the Moora Moora channel. Aquatic vegetation was often abundant (Table 2), the most common species being water ribbon, *Triglochin procera*, waterwort, *Elatine gratioloides*, and common millfoil. Mud was the predominant substrate.

YARRA PIGMY PERCH

Yarra pigmy perch, *Nannoperca obscura* (Klunzinger), was taken from a small swamp in the Wannon Catchment (Fig. 8). Aquatic macrophytes were abundant, with species including common millfoil and water ribbon. The substrate was mud.

MOSQUITOFISH

Mosquitofish, *Gambusia affinis* (Baird & Girard), was found at 12 stations and in both the Wimmera and Glenelg catchments (Fig. 9).

The species was recorded from second to fifth-order streams (Table 3) and was most common in the low-lying areas of the Glenelg catchment and always in association with pools and slow-flowing backwaters. It was present in the Moora Moora channel. Fifty percent of the stations at which mosquitofish was found occurred in areas partially cleared for agriculture. Aquatic

vegetation, including common millfoil, floating pondweed and arrowgrass, *Triglochin striata*, was often abundant. Mud was the predominant substrate.

MIDGLEY'S CARP GUDGEON

Western carp gudgeon, *Hypseleotris klunzingeri*, has recently (Hoese 1980) been regarded as a complex of three separate species, of which Midgley's carp gudgeon is one. These species have yet to be formally described and identification of the Grampians specimen must be regarded as tentative. Specimens have been lodged with the Australian Museum (catalogue No. I. 21778-001).

Midgley's carp gudgeon was found at 5 stations in the Wannon catchment (Fig. 7) 4 of which were on Dwyer Creek, a small tributary of the Wannon River which flows through open pasture and into Bryan Swamp. The fish were captured in shallow, turbid pools with abundant aquatic macrophytes. The bottom substrate was mud.

EASTERN LITTLE GALAXIAS

Eastern little galaxias, *Galaxiella pusilla* (Mack), was found at 17 stations and in both the Wannon and Glenelg catchments (Fig. 10). It was found in second to fifth-order streams (Table 3) and in several swamps. The species was always associated with shallow, slow-flowing stretches of water and often with abundant aquatic macrophytes including common millfoil and water ribbon. Mud was the predominant substrate.

GOLDFISH

Goldfish, *Carassius auratus* (Linnaeus), occurred at 4 stations, 3 in the Glenelg Catchment and 1 in the Wimmera (Fig. 9). It was found in small, low-altitude tributaries flowing through farmland and always associated with mud-bottomed pools.

TENCH

Tench, *Tinca tinca* (Linnaeus), was found at 6 stations, 5 in the Glenelg and 1 in the Wimmera Catchment

TABLE 3

RELATIONSHIP BETWEEN FISH SPECIES DISTRIBUTION AND STREAM ORDER IN THE GLENELG, WANNON AND WIMMERA CATCHMENTS
Number of sampling stations in each stream order is given in parentheses.

Species	Stream order														
	Glenelg					Wannon					Wimmera				
	1(9)	2(20)	3(15)	4(3)	5(8)	1(1)	2(4)	3(8)	4(8)	5(2)	1(4)	2(8)	3(5)	4(5)	5(0)
<i>Galaxias olidus</i>	6	16	7	1	1		2	1	1	1	3	3	1	2	
<i>Salmo trutta</i>						1	1	1					4	1	
<i>Gadopsis marmoratus</i>		3	2	1	1			2	1					5	
<i>Perca fluviatilis</i>		3	6	1	3							1		3	
<i>Philypnodon grandiceps</i>			1		1									3	
<i>Nannoperca australis</i>		2	2	2	3		1	2	1			1		1	
<i>Gambusia affinis</i>		1	2	1	6							1			
<i>Hypseleotris</i> sp. 4							1	2	1						
<i>Galaxiella pusilla</i>		1	3		3		1	1	1					1	
<i>Carassius auratus</i>		1	1		1										
<i>Tinea tinea</i>		1			2										
Minimum no. of spp.	0	0	0	2	2	1	0	0	0	1	0	0	1	1	
Maximum no. of spp.	1	4	3	4	5	1	2	2	3	4	1	2	1	5	
Mean no. of spp.	0.7	1.4	1.8	3.0	2.9	1.0	1.0	1.0	1.0	2.5	0.7	0.7	1.0	2.8	

(Fig. 4). It was always found in pools with mud being the predominant substrate.

RAINBOW TROUT

One specimen of rainbow trout, *Salmo gairdnerii* Richardson, was captured in Lake Wartook (Fig. 4).

CLUSTER ANALYSIS OF SAMPLING SITES

To include data from those sites where southern pigmy perch was only provisionally identified, Yarra and southern pigmy perch were treated as a single taxon in the cluster analysis. Mountain galaxias was the only species recorded at 26 stations, thus forming an obvious grouping prior to the cluster analysis. So that the result was not unduly influenced by this group, only one of these 26 stations was included in the analysis.

The analysis grouped the sites into two main classes, with several subclasses evident (Fig. 11).

Class 1

Sites on generally permanent, clearly defined watercourses or reservoirs where predominant substrates were gravel, bedrock and sand. Aquatic vegetation was not often abundant. Six native species; freshwater blackfish, flathead gudgeon, pigmy perches, mountain galaxias and eastern little galaxias, and six introduced fishes; brown trout, rainbow trout, redfin, tench, mosquitofish and goldfish, occurred in this class.

Subclass A: Sites on low-gradient sections of the Wannon River and on Fyans Creek and MacKenzie River on the Wimmera system. Predominant substrates were gravel, bedrock and sand. Aquatic vegetation was often abundant (Table 4). The sites were well-shaded with eucalypt forest and cover, in the form of undercut banks and fallen timber, was abundant. Freshwater blackfish was the predominant species with brown trout and flathead gudgeon also present.

Subclass B: Sites on headwater tributaries of the Wannon, Glenelg and Wimmera systems not containing trout. The gradient was generally steep with bedrock and sand the predominant substrates and aquatic vegetation seldom abundant (Table 4). Sites were generally well-shaded by eucalypt forest and mountain galaxias was the dominant species (Fig. 12), being the only fish present at 26 of the 31 sampling stations. The only other fish occurring in this subclass was the freshwater blackfish.

Subclass C: Generally low-gradient sites (Table 4) on the main channels of the Wannon, Glenelg and Wimmera systems, flowing through open woodland, often with quiet backwaters and abundant aquatic vegetation. Sand and mud were the predominant substrates (Table 4). The Moora Moora and Wartook Reservoirs occurred in this grouping. Redfin was the dominant species (Fig. 12). Other fishes present were brown trout, rainbow trout, tench and the smaller species; goldfish, mosquitofish, mountain galaxias, eastern little galaxias, pigmy perch and flathead gudgeon.

Subclass D: Sites on the high altitude, generally steep-gradient headwaters (Table 4) of the Wannon River and Fyans Creek in the Wimmera system. Gravel, boulders and bedrock were the dominant substrates and aquatic vegetation was not often abundant (Table 4). Sites were generally well-shaded by eucalypt forest and brown trout was the only species present.

Class 2

Sites on swamps, isolated pools and watercourses of indeterminate drainage in open woodland or cleared grassland. Many sites were ephemeral, drying up in summer. Sand and mud were the predominant substrates and aquatic vegetation was often abundant (Table 4). The fish fauna consisted entirely of small species: six



Figs 7-10—Distribution of flathead gudgeon, *Philypnodon grandiceps*, and Midgley's carp gudgeon, *Hypseleotris* sp. 4 (7), Southern pigmy perch, *Nannoperca australis*, and Yarra pigmy perch, *Nannoperca obscura* (8), Mosquitofish, *Gambusia affinis* and goldfish *Carassius auratus* (9), and eastern little galaxias, *Galaxiella pusilla* (10) in the Grampians Region. Boundaries (....) of the Glenelg, Wannon and Wimmera River catchments are shown.

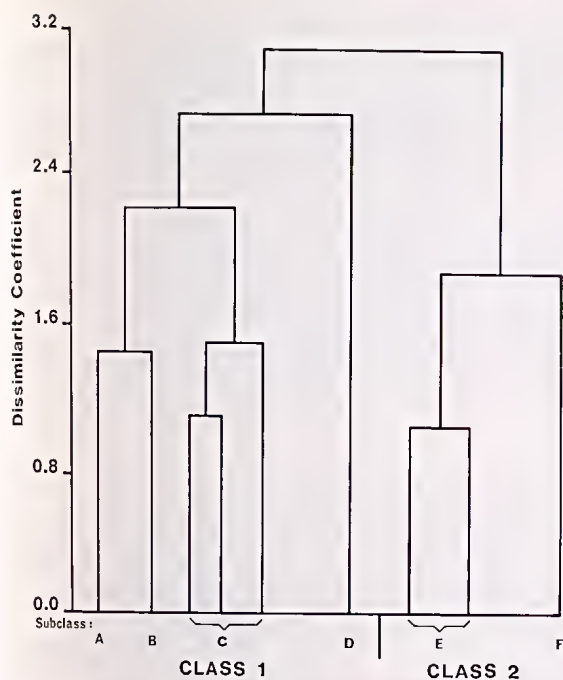


Fig. 11—Cluster analysis of sampling sites according to presence or absence of fish species.

native; pigmy perches, eastern little galaxias, mountain galaxias, Midgley's carp gudgeon and flathead gudgeon, and two introduced species; mosquitofish and goldfish.

The analysis indicated two subclasses (Fig. 11) with pigmy perch the dominant species in subclass E and eastern little galaxias the dominant species in subclass F (Fig. 12). No major physical differences were apparent among the sites although pigmy perch did not occur at any of the sites in subclass F.

DISCUSSION

Stream order analysis has been used by biologists in the Northern Hemisphere to investigate the distributions of fishes within river systems (Kuehne 1962, Harrel *et al.* 1967, Whiteside & McNatt 1972, Lotrich 1973) but has been used little in Australia (see Cadwallader 1979, Jackson & Williams 1980). In the present study, with the possible exception of mountain galaxias, which occurred most frequently in second and third-order streams (Table 3), there were no obvious distributional patterns related to stream order. The mean number of species per station did increase with increasing stream order (Table 3), probably reflecting an increase in diversity of available habitat, but the distribution of fishes in the Grampians Region may best be explained in terms of their habitat requirements.

Cluster analysis shows that sampling sites (Fig. 11) can be grouped according to their faunal assemblages and, furthermore, that these groupings do correspond to broad habitat types (Table 4). The most apparent differences are between those sites occurring on the more permanent, well defined watercourses (class 1 in Fig. 11) and those occurring on swamps, isolated pools (often of

temporary nature), and areas of indeterminate drainage (class 2 in Fig. 11). The larger native and introduced fishes were only found at those sites in class 1 and the greatest diversity of fishes occurred in subclass C (Fig. 11) where the two habitat types overlap. In the overlap area, permanent waterways were combined with quiet, shallow backwaters often with abundant aquatic vegetation. The main channels provided suitable habitat for the larger fishes such as redfin, tench and freshwater blackfish and the backwaters contained the smaller species such as pigmy perch and eastern little galaxias.

Within those sites in class 1, fishes are further distributed according to their habitat preferences, illustrated by the dominant species in each particular subgroup (Fig. 12).

The preferred habitat of the freshwater blackfish is a slow-flowing section of river with abundant cover in the form of submerged logs, boulders or undercut banks (Jackson & Llewellyn 1980) and they were the dominant species in subgroup A (Fig. 12).

The mountain galaxias is primarily a small-stream species (McDowall 1980a) that penetrates the highland tributaries. It was the dominant species in subclass B (Fig. 12), a group of sites on headwater tributaries of the Wannon, Glenelg and Wimmera rivers.

Redfin is a species of still or slow-flowing waters, particularly where aquatic vegetation is abundant (McDowall 1980b). It was the dominant species in subclass C (Fig. 12), especially in those sites in the slower-flowing areas of the Glenelg River.



Fig. 12—Percentage occurrence of each fish species within each subclass identified by cluster analysis.

TABLE 4
SUMMARY OF THE ALTITUDE, GRADIENT, SUBSTRATE TYPE AND ABUNDANCE OF AQUATIC VEGETATION OCCURRING IN EACH SUBCLASS IDENTIFIED BY CLUSTER ANALYSIS

Class	Subclass	No. of Sites	Altitude		Gradient		% of stations with a particular substrate type dominant					% of stations with abundant aquatic vegetation
			Mean \pm S.D.	Range (m)	Median* (m/km)	Range (m/km)	G	B	BD	S	M	
1	A	5	276 \pm 46.6	220-320	4.6	2.7- 10.5	40		20	20	20	75
	B	31	317 \pm 104.0	200-600	28.6	2.1-100.0	10		40	37	13	3
	C	21	260 \pm 84.3	150-460	3.4	0.0- 28.6	12	2		45	40	52
	D	7	394 \pm 78.9	320-560	28.6	11.8-133.3	36	21	29	7	7	14
2	E	26	229 \pm 30.2	200-270	0.6	0.0- 50.0	2	2		11	85	73
	F	5	212 \pm 22.8	180-240	1.9	0.0- 3.3			10	30	60	60

G, gravel; B, boulders; BD, bedrock; S, sand; M, mud.

* Due to the wide range of gradients recorded, the median rather than the mean value has been given.

Brown trout is restricted to cool, well-oxygenated waters and requires a gravel substrate and flowing water for reproduction (McDowall & Tilzey 1980). It was the only species present at the sites in subclass D, all of which were on the upper reaches of the Wannon River and Fyans Creek. Small trout (<50 mm total length) were present, suggesting that these trout populations are self-sustaining.

The relationships between the native and introduced fishes in Class 1 sites are difficult to ascertain but it would appear that mountain galaxias and brown trout do not co-exist. Mountain galaxias clearly dominate the headwater tributaries of all three river systems with the exception of the upper reaches of the Wannon River and Fyans Creek where brown trout occur. Mutually exclusive distributions of brown trout and mountain galaxias in highland streams on mainland Australia have been documented by several authors (Tilzey 1976, Cadwallader 1979, Fletcher 1979, Jackson & Williams 1980) and the distribution of these two species in the Grampians provides another example.

There were many sites on the headwater tributaries of the Glenelg River, containing mountain galaxias, which appear suitable for brown trout. The low-lying, swampy areas of the Glenelg River probably form a barrier preventing trout from Rockland Reservoir penetrating these tributaries, particularly in the summer when temperatures are high and oxygen concentrations low.

The sites within class 2 are dominated by pigmy perches and the eastern little galaxias, species which inhabit still waters with abundant aquatic vegetation (McDowall 1980c, Llewellyn 1980). The distribution of fishes within these sites must vary significantly seasonally as the shallow areas of swamp and backwater expand and contract. McDowall (1980a) has suggested that the eastern little galaxias may be able to aestivate but this has yet to be proven.

There is no evidence to suggest that the distribution of any of the native fishes in these still water areas have been affected by the introduction of exotic species. The native fishes occurred in most areas where the habitat

was suitable. The clearing of land in some low-lying areas has had a visibly obvious effect on the aquatic habitat through the removal of shade vegetation, siltation and erosion caused by increased run-off. Twenty-nine percent of the stations occurring in cleared agricultural land contained no fish, compared with only 12 percent for all other stations.

The fact that only 7 native fishes were captured in the Grampians Region is typical of inland waters in Victoria, and reflects the generally depauperate nature of the fauna (Lake 1971, 1978, McDowall 1980c). The Grampians contain no single species or faunal assemblage not present elsewhere in Victoria, however, they do contain examples of several types of aquatic habitat that remain in a relatively pristine state. For example, many of the small tributaries of the Glenelg, remain relatively untouched and the region contains extensive areas of shallow swampland, examples of which are in increasing danger of being cleared and drained elsewhere in Victoria.

The results of the present survey could not be directly compared with those of Emison *et al.* (1978) as many of their data were drawn from sources other than the results of field surveys. However, they do record the presence of the eastern little galaxias at Greens Creek (station 34 in our survey) and suggest that this provides an opportunity for the preservation of a population of this species.

The eastern little galaxias occurs in other localities in Victoria but is particularly vulnerable to habitat alteration. Our results show that the species is widespread in the low-lying, swampy areas of the Grampians Region (Fig. 10) and that the area does indeed provide a unique opportunity to preserve examples of the habitat of this species.

The Moora Moora Channel, directing water from the Glenelg to the Wimmera System, and a pipeline which directs water from the upper reaches of the Wannon northwards into the Fyans Creek Catchment could enable fishes in the Grampians Region to move outside their natural ranges. The natural distribution of eastern little galaxias, for example, is limited to coastal

drainages. It occurred at a number of stations in the Glenelg River and was present in a drain emptying directly into the Moora Moora Reservoir (station 38). From there it would be possible for the species to enter the Moora Moora Channel and hence the Wimmera System.

ACKNOWLEDGEMENTS

We would like to thank John McKenzie, Mark Nelson and Sue Beattie who assisted in the field. We also thank Alicia McShane who drew the figures, Doug Hoese, Australian Museum, Sydney, who identified the specimens of Midgley's carp gudgeon and Mike Mobley who undertook the cluster analysis.

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APPENDIX

Details of Sampling Stations in the Grampians Region and Fishing Method(s) used at each station. E, Electrofishing; D, Dip-netting; N, Gill-netting. Gl, Glenelg; Wa, Wannon; Wi, Wimmera. * Sites revisited in April 1980.

Station No.	Map No.	Reference	Altitude (m)	Gradient (m/km)	Stream order	Sampling method
1* Wi	7324	XE201184	180	5.4	2	E,D
2 Wi	7324	XE272127	200	200.0	2	E
3 Wi	7324	XE256122	360	9.5	2	E
4 Wi	7324	XE301086	200	6.9	3	E
5 Wi	7324	XE313048	220	22.2	2	E
6 Wi	7323	XE269024	320	133.3	1	E
7 Wi	7323	XE299002	460	4.2	2	E
8 Wi	7323	XE301002	460	4.9	1	E
9 Wi	7323	XD286967	440	0.0	Reservoir	N
10 Wi	7323	XD297932	460	8.3	2	E
11 Wi	7323	XD294929	460	10.0	2	E
12 Wi	7323	XD265920	440	12.5	4	E
13 Wi	7323	XD255900	460	25.0	1	E
14 Wi	7323	XD223946	240	10.5	4	E
15 Wi	7323	XE191004	200	2.8	4	E
16 Wi	7323	XD161929	260	18.1	2	E
17* Wi	7323	XE159008	200	0.0	Swamp	D
18 Gl	7323	XD226909	400	20.0	1	E
19 Gl	7323	XD213900	380	25.0	2	E
20 Gl	7323	XD227872	280	28.6	3	E
21 Gl	7323	XD311815	600	66.7	1	E
22 Gl	7323	XD281861	300	28.6	2	E
23* Gl	7323	XD258848	250	7.1	3	E
24* Gl	7323	XD212846	240	2.9	3	D
25* Gl	7323	XD206840	240	2.9	3	D
26 Gl	7323	XD171869	260	33.3	2	E
27* Gl	7323	XD180844	220	0.0	Swamp	D
28 Gl	7323	XD169863	260	25.0	1	E
29 Gl	7323	XD143635	300	28.6	2	E
30 Gl	7323	XD172659	300	28.6	3	E
31* Gl	7323	XD201671	260	5.4	2	D
32* Gl	7323	XD209694	250	4.6	4	E,D
33 Gl	7323	XD208697	260	100.0	1	E
34 Gl	7323	XD233702	240	3.4	2	E,D
35 Gl	7323	XD281690	250	11.1	2	E
36 Gl	7323	XD324717	320	50.0	3	E
37 Gl	7323	XD324716	320	50.0	1	E
38 Gl	7323	XD259739	220	0.4	Drain	E,D
39* Gl	7323	XD293746	230	3.8	4	D
40 Gl	7323	XD322728	280	66.7	2	E
41 Gl	7323	XD315748	260	66.7	2	E
42 Gl	7323	XD305769	280	23.5	2	E
43 Gl	7323	XD298779	280	40.0	1	E
44 Gl	7323	XD290786	260	66.7	1	E
45 Gl	7323	XD294809	480	40.0	2	E
46* Gl	7323	XD281782	230	12.1	2	E
47 Gl	7323	XD267808	240	12.5	2	E
48 Gl	7323	XD253793	220	0.0	Reservoir	N
49* Gl	7323	XD248789	220	0.4	Drain	E
50 Gl	7323	XD211766	240	33.3	1	E
51 Gl	7323	XD187809	220	0.6	5	D
52 Gl	7323	XD188805	220	0.6	5	N
53 Gl	7323	XD121859	210	0.6	5	D
54 Gl	7323	XD112878	210	0.6	5	E
55* Gl	7323	XD056936	220	0.6	5	D
56 Gl	7323	XD054921	220	0.6	5	N
57 Wi	7324	WE962092	170	0.0	Swamp	D

APPENDIX (Continued)

Station No.	Map No.	Reference	Altitude (m)	Gradient (m/km)	Stream order	Sampling method	
58	G1	7323	XD113815	260	22.2	1	E
59	G1	7323	XD110793	240	16.7	2	E
60	G1	7323	XD068847	220	2.5	2	D
61	G1	7323	XD058771	200	4.1	3	D
62	G1	7323	WD981883	220	4.1	3	E, D
63	G1	7323	WD984838	200	0.6	3	E
64	G1	7323	XD169780	540	28.6	2	E
65	G1	7323	XD152776	460	13.3	3	E
66	G1	7323	XD126760	230	22.2	2	E
67	G1	7323	XD124748	240	10.0	2	E
68	G1	7323	XD106729	220	3.3	2	E
69	G1	7323	XD083666	280	33.3	1	E
70	G1	7323	XD071649	280	50.0	2	E
71*	G1	7323	XD063696	220	2.7	3	D
72	G1	7323	XD057696	220	2.7	3	E
73*	G1	7323	XD027703	210	0.0	Swamp	D
74	G1	7323	XD007670	220	2.1	3	D
75	G1	7323	XD057730	200	2.3	4	E, D
76*	G1	7223	WD752877	150	0.9	5	E, D
77	G1	7223	WD749772	180	0.6	5	D
78	G1	7223	WD769715	200	3.3	3	E
79	G1	7223	WD793663	230	4.1	3	E
80	Wa	7223	WD866516	220	2.8	4	D
81	Wa	7323	WD909559	230	2.1	4	D
82	Wa	7323	WD908553	230	2.1	4	E
83	Wa	7323	XD061627	260	44.4	2	E
84*	Wa	7323	XD037623	230	0.0	Swamp	D
85*	Wa	7323	XD029546	220	0.8	3	D
86	Wa	7323	WD996528	220	5.4	3	E
87	Wa	7323	XD052537	230	5.5	3	E
88*	Wa	7323	XD298634	280	8.7	2	D
89*	Wa	7323	XD285632	270	0.0	Swamp	D
90*	Wa	7323	XD255610	260	3.7	4	D
91	Wa	7323	XD244573	220	1.9	4	D
92	Wa	7323	XD242570	220	1.9	4	E
93	Wa	7323	XD223579	240	1.8	3	D
94	Wa	7323	XD222585	240	1.8	3	E
95	Wa	7323	XD233586	240	0.0	Swamp	D
96	Wa	7323	XD197561	240	5.0	2	E
97	Wa	7423	XD352700	400	11.8	3	E
98	Wa	7423	XD346618	380	44.4	2	E
99	Wa	7423	XD332653	320	4.6	4	E
100	Wa	7423	XD333625	320	8.7	3	E
101*	Wa	7423	XD304558	280	2.7	4	E
102*	Wa	7322	XD216375	240	1.2	4	E
103*	Wa	7322	XD162389	220	0.0	Swamp	D
104*	Wa	7322	XD119414	200	0.0	Swamp	D
105*	Wa	7322	XD062459	200	0.1	5	E, D
106	Wa	7322	WD929472	200	0.1	5	D
107	Wa	7323	XD113577	260	18.2	3	E
108	Wi	7423	XD364730	400	28.6	3	E
109	Wi	7423	XD363772	360	28.6	3	E
110	Wi	7423	XD374788	340	133.3	3	E
111	Wi	7423	XD368800	280	9.1	4	E
112	Wi	7423	XD357818	320	28.6	3	E
113	Wi	7323	XD324861	560	66.7	1	E
114	Wi	7323	XD327862	520	66.7	2	E
115	Wi	7423	XD351894	220	3.6	4	E





PROCEEDINGS
OF THE
ROYAL SOCIETY OF VICTORIA

Volume 95

NUMBER 2

ROYAL SOCIETY'S HALL
9 VICTORIA STREET, MELBOURNE 3000

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THE BATHYMETRY OF LAKES KING AND VICTORIA

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ABSTRACT: This report describes a recent bathymetric survey of part of the Gippsland Lakes. Charts giving the results are included.

The point at which rivers debouche is almost always of interest, being frequently the site of commercial, recreational and environmental activity with all the conflicts implied by these concurrent uses. These regions are of special interest to the engineer since the whole nature of the estuary is determined by a number of hydraulic forces in delicate balance so that quite small changes can have dramatic consequences. The estuaries around the southeast coast of Australia, from Lake Alexandrina to Malacoota Inlet and beyond, are unusual, and comprise a lake communicating with the sea across a narrow, variable sand bar. They may be cut-off from the sea by the sand bar for large parts of the year. One of the largest of these, and quite the most complex, is at Lakes Entrance in Victoria. The mouth of this estuary, at Lakes Entrance, is artificially stabilised and maintained open throughout the year. Notwithstanding the commercial and scientific interest of this system, there has been surprisingly little modern systematic measurement of its parameters.

The Department of Mechanical Engineering at Monash University, however, has been studying the lake system both theoretically and observationally. In particular, it has been conducting extended student excursions to the region for more than ten years, and this report gives some initial observations of bathymetry obtained on those trips. There appears to have been no general survey of the depths in the Lakes since the fine work of Mason 1893-95. This covers only Lake King and the western half of Lake Victoria (Mason 1895). More recently, the State Electricity Commission of Victoria has surveyed Lake Wellington (SEC 1972a) and, rather sparsely, the western end of Lake Victoria (SEC 1972b). The Ports and Harbours Division of the Public Works Department, Victoria, is conducting a survey of a large part of the lake system. There are no published recent data for Lake King. To remedy this deficiency we have, during 1979 and 1980, surveyed the whole of Lakes Victoria and King.

SURVEY METHODS

These surveys were made using the Department's 8 m aluminium boat. Depths were measured with a Raytheon DB819 echo-sounder; the resolution and probable accuracy of measurement is 0.1 m. Depth readings from the echo-sounder were first corrected for the depth of immersion of the echo-sounder. They were then converted to AHD by linear interpolation between two or three specially established tide gauges which were connected by short closed levelling traverses to bench

marks. Location is a problem throughout the Lakes as the shores are (navigationally) rather featureless. We did not have access to radio-location equipment for these surveys and have had to rely on traditional methods, augmenting the natural landmarks with buoys and, for the Lake King survey where the problems are particularly acute, with balloons tethered at known points. Sightings, which were made using both compass and sextant, were taken at the beginning and end of each traverse, which the boat attempted to cover at uniform velocity, and at one or two intermediate points as a check on the navigation. Intermediate positions were then located by interpolation. Overall, we estimate the maximum error in position to be 20 m nearshore and 50 m far from shore with typical values being less. There is, indeed, greater uncertainty about the location of the shoreline in some parts of our maps than this.

The echo-sounder used a frequency of 208 kHz ensuring a clear reflection from the upper surface of the bed, whether the latter was silt or sand. In a few localities echoes were obtained from weed or even detritus on the bed but in these cases the bed was still readily identifiable. Comparison tests between lead-line and echo-sounding did not show differences as even the silt bed was firmly consolidated.

PROCESSING OF OBSERVATIONS

All the depth data obtained have been stored digitally, the coordinates of each sounding being converted automatically from the field plotting sheets on an x-y digitising table. Each data set is held as a separate file, and so can be plotted selectively. The coastline of the entire system, referred to the same coordinates, is also stored digitally. We can thus call up details of any part of the Lakes. Figures 1-3 are copied directly from the computer output.

BATHYMETRY

The SECV measurements in Lake Victoria are included in Figs 1 and 2; the agreement with our survey is good, but the floor is fairly uniform so this is not a very critical test. Our survey of Lake King is shown in Fig. 3, and our points are compared with (every 4th of) Mason's points. The overall impression is that the values have changed very little, which refutes the canard that there has been a secular change of depth in the Lakes in the past 100 years.

However, closer examination shows some systematic variations. While no modern measurements are significantly shallower than Mason's, locally they may be

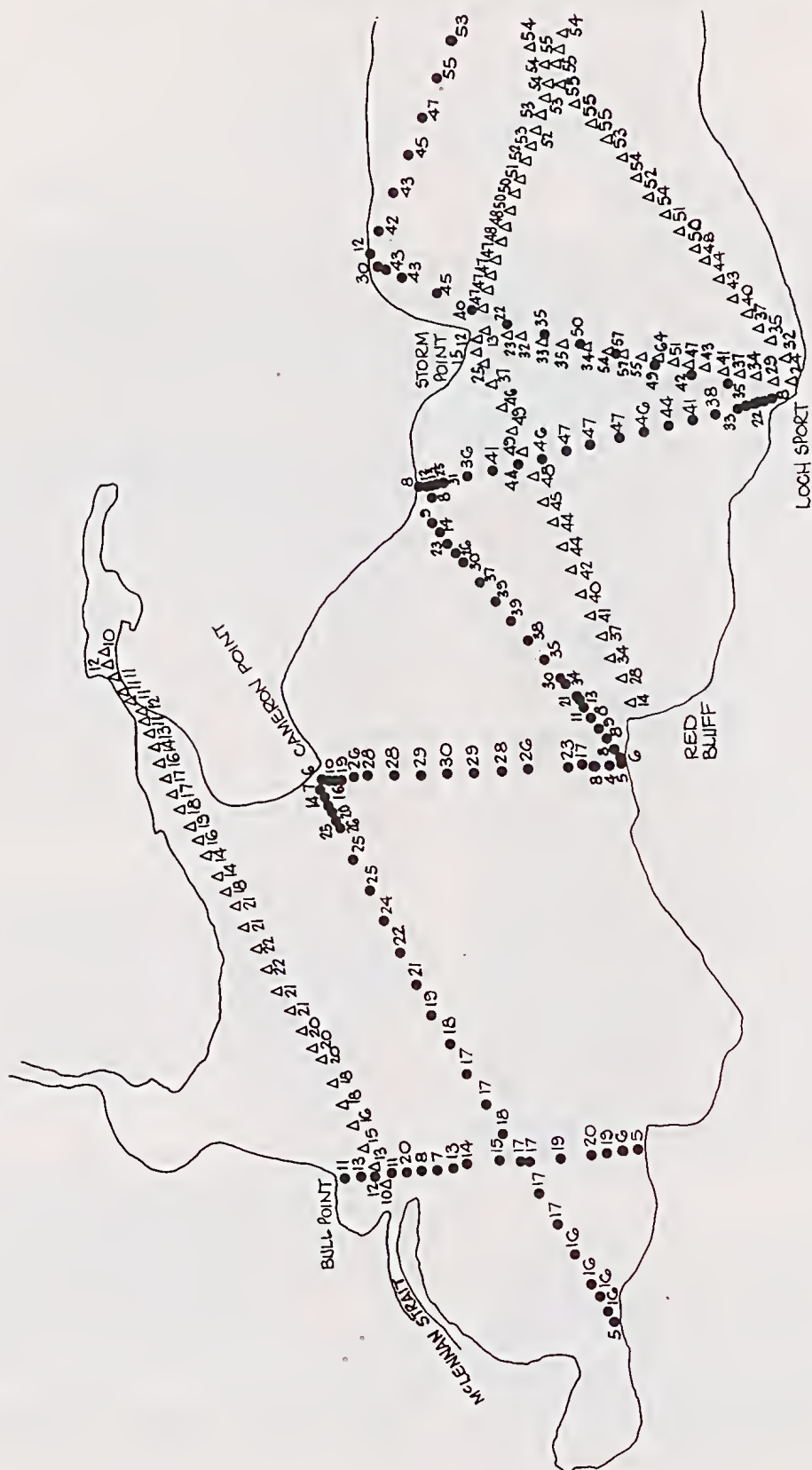


Fig. 1—Lake Victoria, western half—modern bathymetry. Depths in decimetres, SEC Δ ; Monash \bullet .

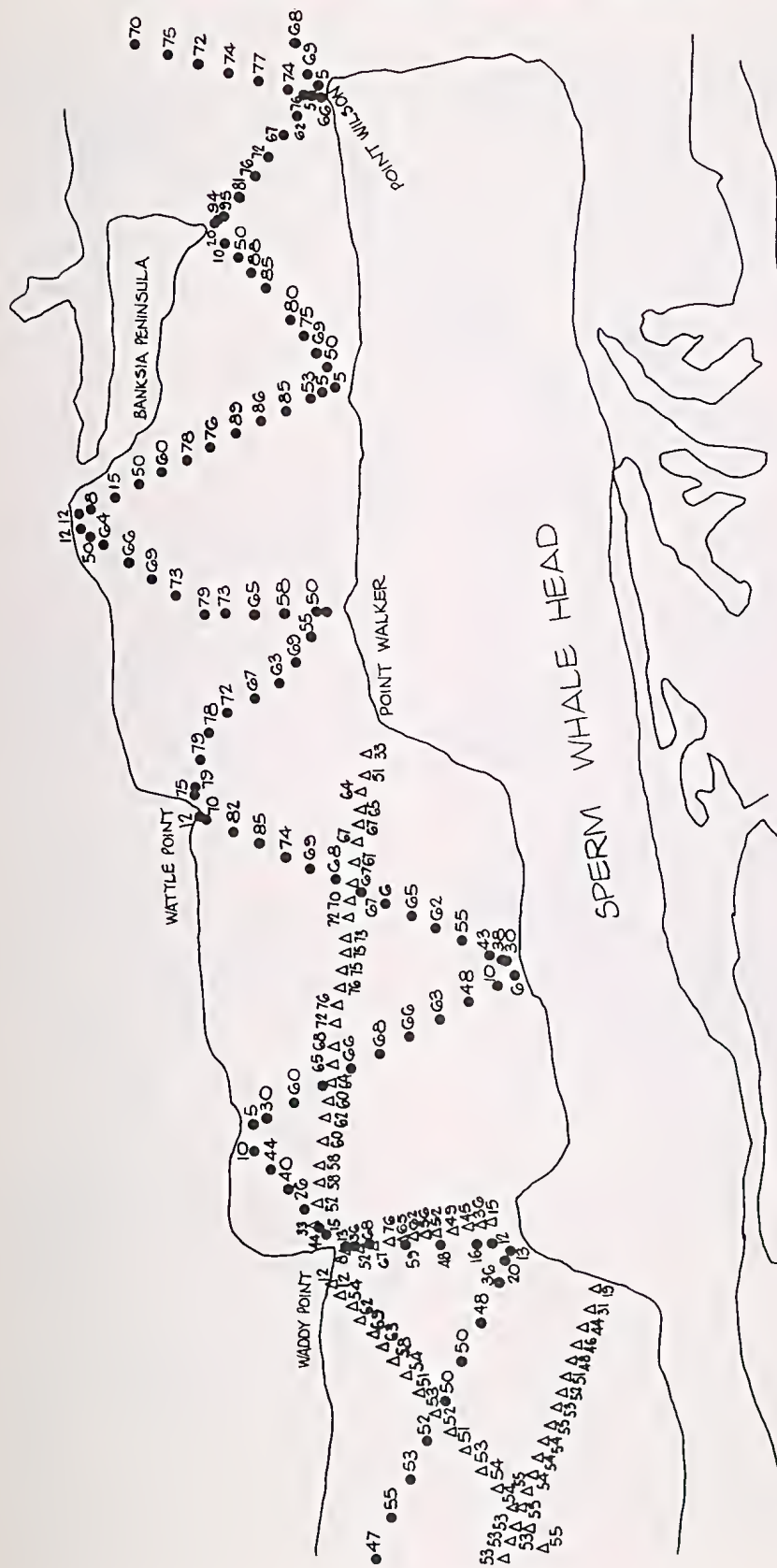


Fig. 2—Lake Victoria, eastern half—modern bathymetry. Depths in decimetres. SEC Δ; Monash ●.

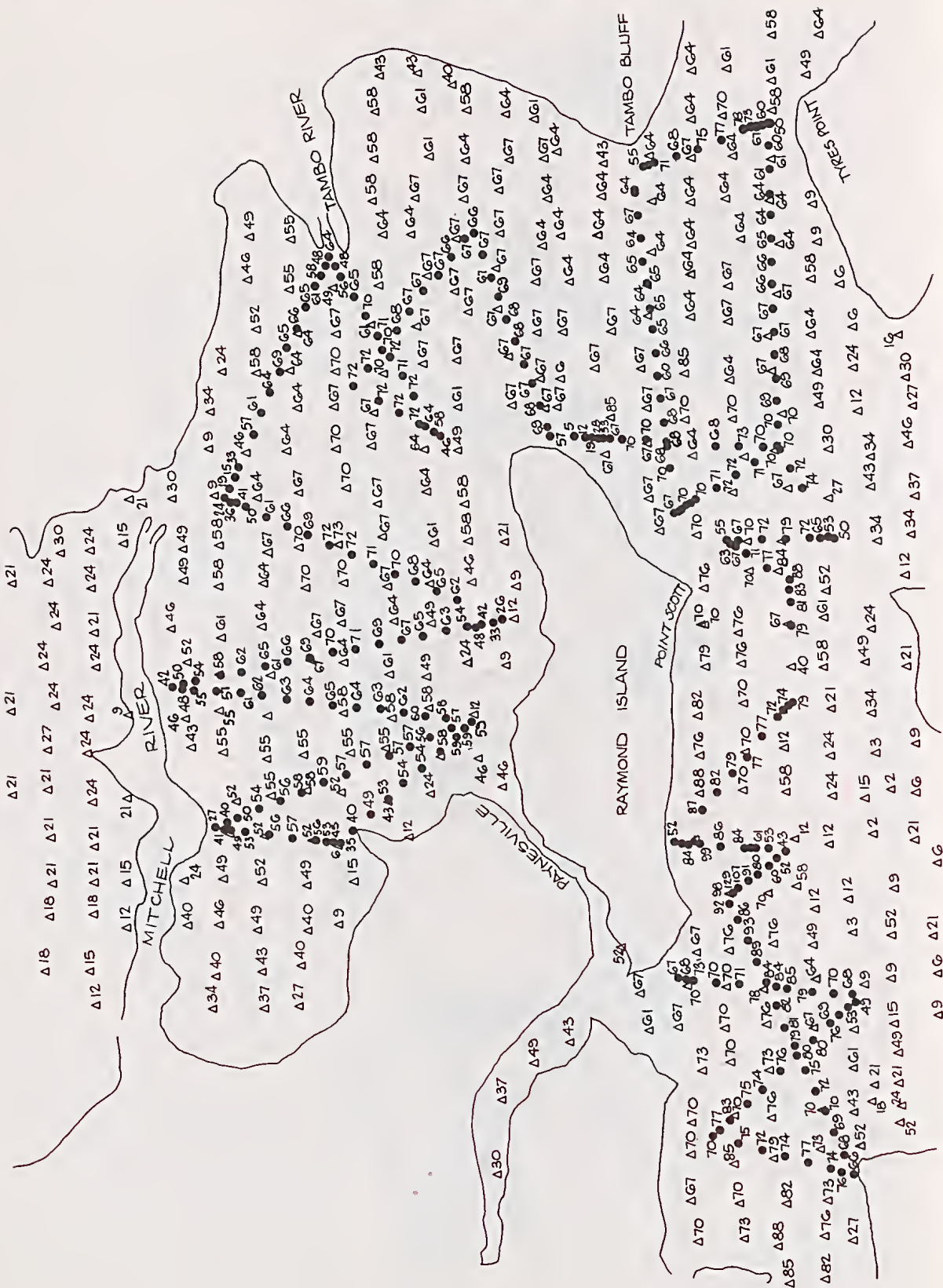


Fig. 3—Lake King—surveys of 1980 and 1993. Depths in decimetres. SEC Δ; Monash ●.

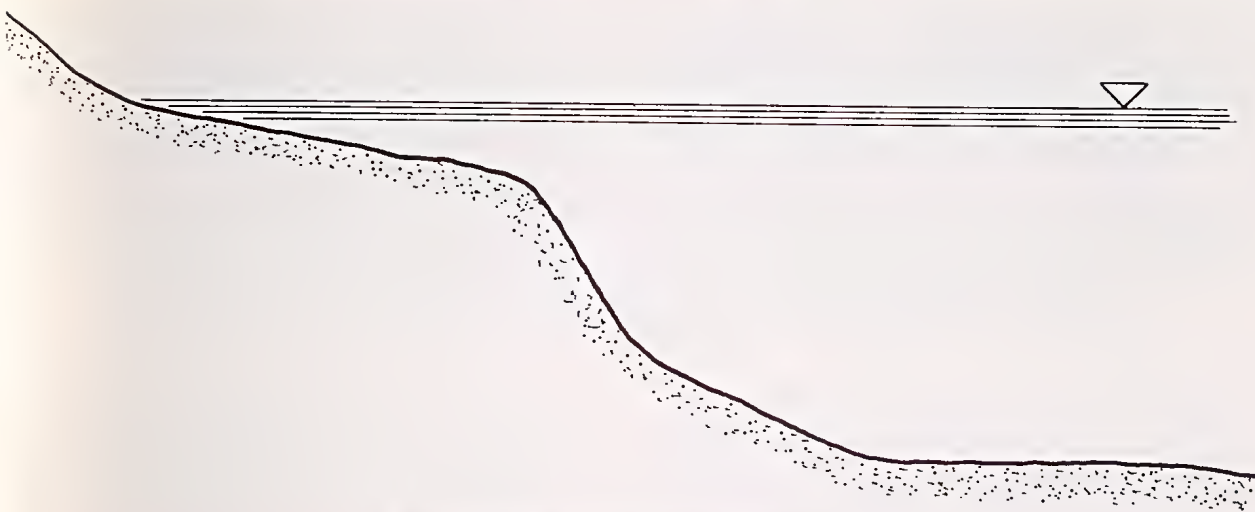


Fig. 4—Profile of the bed of Lake Victoria.

deeper. Thus, the channel at the entrance to the Tambo seems to be 0.5 m deeper; there is a new depression north of Raymond Island and off Point Scott. If it is supposed, then, that the broad areas of agreement indicate a situation stable since 1895, these deeper areas must represent bottom sediment carried away. This effect presumably results from the continuous flushing regime operating since the entrance has been kept open, coupled with the sharper flood peaks in the tributary rivers caused by more intensive settlement and land clearing. These measurements, unhappily, are not dense enough to estimate reliably how much material may have been lost in this way. Mason's survey was made just after the present entrance was dredged and stabilised, so we have no data on conditions prior to that. However, collateral evidence from the echo-sounder does give an indication of some aspects of the long term history of the lake system, which we take up below.

MORPHOLOGY

The profiles obtained in traversing display a characteristic cross-section for Lake Victoria shown in Fig. 4. From the shoreline there is gradual slope of about 1 in 150 out to a depth of about 1 m. The depth then drops very sharply to about 2.5 m before continuing on a slope of about 1 in 7 down to 3 m. The bed then becomes flat or slopes very gently down to its maximum depth of 3-6 m depending upon the position of the traverse within Lake Victoria. This break in slope appears very consistently and would seem to indicate a wave-cut step; however, the evidence of the echo-sounder suggests otherwise. The echo-sounder was operated on full gain, utilising a high-powered narrow-beam transducer, with the result that weak echoes were received from layers of sediment below the bed of the Lake. These echoes showed that the strata which form the uppermost, gradually sloping, section are continuous with those forming the steeper section. The lower gradually sloping or horizontal bed consists of

layers of sediment laid above these steeply dipping strata.

The frequency of the echo-sounder was not chosen for sub-bottom profiling, and only small penetration of the bed was possible. Furthermore, the penetration of the bed achieved far from the shore did not result in coherent echoes. The latter result was also obtained by King (1980) utilising a much lower, and hence more suitable, frequency. King decided that gas bubbles within the deposited sediments were producing an incoherent back-scatter and preventing information on the underlying strata being obtained by acoustic techniques. King also showed, for the two or three sounding traverses which extended from the nearshore to the deeper waters, that the strata forming the steeply sloping sections of the channel bed appeared to dive below the strata forming the generally horizontal, central part of the bed.

The inference to be drawn from the echo sounding is that gradual deposition of silt occurred on the steeply sloping faces of natural levees and on the margins of the lakes. Since then, the lakes have been the site of gradual deposition of fine sediment and organic material deposited in relatively horizontal strata resting unconformably on the steeper strata. A more tranquil situation with a lower total sediment load seems likely in this later regime.

The small scale features on the echo-sounder traces were examined, but no evidence of sand dunes or sand waves was found in Lake Victoria. There were differences in the strength of the returned echo and in the noise accompanying the return, indicated by the length and regularity of the dashed line the upper surface of which describes the sea bed. Attempts were made to correlate the nature of the returned echo with the texture of the sea bed, as determined by sampling the sediment and by observing the presence or absence of weed. A rather subjective correlation was obtained and confirmed that the shallow gradual slope of the lake

(near the shore) was weed covered on most traverse lines while the deeper gradual slope was not covered by weed, and in fact was bare silt in most cases. This technique of determining the nature of the bottom from interpretation of the echo-sounder traces warrants further study.

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PROMANAWA GEN. NOV., AN AUSTRALIAN MIOCENE PUNCIID OSTRACODE FROM HAMILTON, VICTORIA

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ABSTRACT: *Promanawa australiensis* gen. nov. et sp. nov. is described from the Miocene of Hamilton, Victoria. This is the first confirmed record of the Punciidae from Australia. The affinities, biology and biogeography of punciids are discussed. A neotype is designed for *Puncia novozealandica* Hornibrook 1949.

The Punciidae is a family of Cenozoic Ostracoda showing remarkable similarities in shape and ornament to some frilled Palaeozoic taxa (Hornibrook 1949). They are already recorded from the Miocene of Australia on the basis of a personal communication from J. W. Briggs, Jr. (cf. McKenzie 1967, p. 232). Our specimen from near Hamilton (Fig. 1), however, is the first confirmation of their occurrence on this continent. Numerous and lengthy searches of Miocene washings by one of us (K.G.M.), especially in the Balcombe Clay, from Mornington, Victoria, has failed to yield any material other than fragments.

The single valve on which our new genus and species is based is excellently preserved. We feel confident, therefore, that formal description of this unique specimen will not lead to subsequent confusion regarding the taxon.

SYSTEMATIC PALAEONTOLOGY

Family PUNCIIDAE Hornibrook 1949

Genus *Promanawa* nov.

TYPE SPECIES: *Promanawa australiensis* sp. nov.

ETYMOLOGY: *Pro*(L.)=before, and genus name *Manawa*; the species name is derived from Australia.

DIAGNOSIS: Punciid characterised by a coarse, well raised surface reticulation, an irregular dorsal margin, and the absence of lunettes on the ventral frill. Adductor muscle scars 6 in number, biserial; with about 30-40 radial (marginal) pore canals; normal pore canals few, simple and raised but not rimmed.

COMPARISON: *Promanawa* differs from *Manawa* Hornibrook 1949 most obviously by the coarse, well raised surface reticulation; in *Manawa* the reticulation is nearly flush with the surface. Further, the lunettes which characterise the ventral frill of *Manawa* do not occur in our new genus. Examination of the types of *Manawa tryphena* (Auckland Museum AM/0 84a,b) indicates that, like *Promanawa*, it has a single mandibular scar. But, unlike *Promanawa*, the main dorsal scar of *Manawa* does not lie on a prominent internal node. The radial pore canal pattern of *Promanawa* closely resembles that of *Puncia* Hornibrook 1949, the only other punciid genus yet known. However, *Puncia* has a smooth to micropunctuate and nonreticulate shell.

Unfortunately, the holotype of *Puncia novozealandica* Hornibrook 1949 was destroyed by another worker. We therefore designate as the neotype the remaining specimen from the original material, (Hornibrook 1949, pl. 50, fig. 4), a juvenile valve (Auckland Museum AM/0 85a) from, "Mestayer Stn, 7, 98 faths., off Big King" (Hornibrook 1949, p. 470).

Promanawa australiensis sp. nov.

Figs 2, 3

DESCRIPTION: Carapace broadly axehead-shaped in lateral view; calcareous; moderately inflated; coarsely reticulate, with well raised muri; each solum perforated by several small pores penetrating to the internal surface; relatively large heart-shaped mediodorsal pit housing the adductor muscle scars (which lie on the corresponding internal node); cardinal angles well defined; dorsal margin irregular; ventral margin evenly rounded; retral swing weak; slightly plenate posteriorly; frill broad and delicate, hollow between the septa, with about 40 long radial pore canals, some slightly swollen medially (the radial septa of Hornibrook (1979)). Internally left valve hinge line straight and smooth; ventral margin with prominent inner list, selvage and frill but lacking a vestibule (all pore canals extend to its inner border); normal pore canals few, scattered, simple and raised but unrimmed, occurring at muri intersections; adductor muscle scars of punciid type, numbering 6, arranged biserially (3 + 3) (cf. Ishizaki 1973) and seated on a prominent internal node; no frontal scar; a single mandibular scar present; also a large dorsal scar seated on an internal node, plus a smaller dorsal scar above and slightly in front.

DIMENSIONS OF HOLOTYPE: Left valve, adult male, NMVP74478; length—0.57 mm, height—0.31 mm. Only the holotype is known.

TYPE LOCALITY: Muddy Creek Marl, on the north bank of Grange Burn, opposite Henty's House, near Hamilton, Victoria (Fig. 1).

AGE: Early Middle Miocene (N9) (Bell & Neil 1982).

COMPARISON: The only other species of *Promanawa* is *P. konishii* (Nohara 1976) from Okinawa, originally placed in *Manawa*, which has the coarse well raised reticulation, irregular dorsal outline, numerous ventral radial pore canals that characterise our genus and also lacks

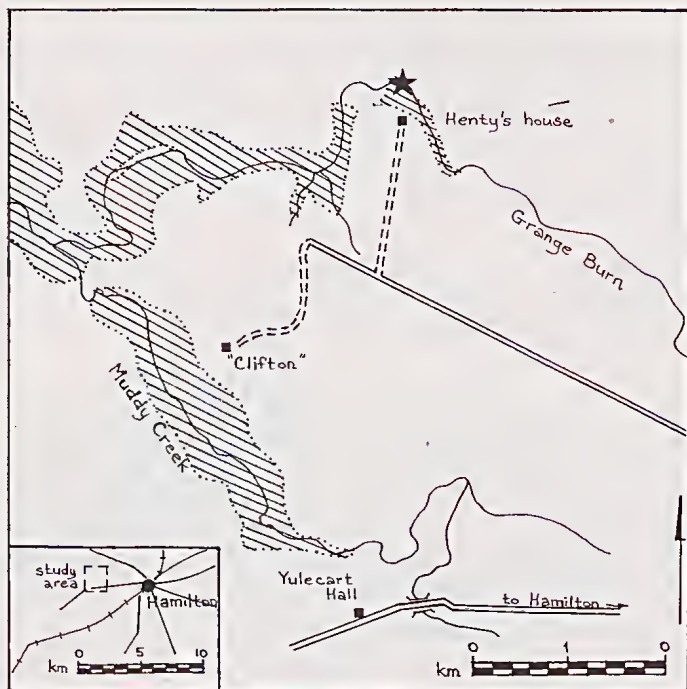


Fig. 1—Locality map of the Grange Burn and Muddy Creek area, near Hamilton, Victoria, indicating the collection site (*) and the extent of Miocene outcrop (hachured).

the ventral frill lunettes typical of *Manawa*. But the heart-shaped pit of *P. australiensis* is not clearly developed in *P. konishii* although it does have a depression in the adductor muscle scars region. *Promanawa australiensis* lacks the feeble papillae which occur on the muri of *P. konishii* and there are only about 30 radial pore canals in *P. konishii* versus about 40 in the Australian species.

DISCUSSION: Punciids are an esoteric group. Their resemblance to beyrichicope Eurychilinaea was recorded by Hornibrook (1949). However, the punciid adductor muscle scar pattern, known for all species described so far (including ours), is a unique type of biserial scar. Later, Hornibrook (1963) noted correspondences between the hingement of *Manawa* and that of the kirkbyacean *Aurikirkbya* Sohn 1950. We note the further correspondence that kirkbyacean adductor muscle scars also lie on an internal node.

Kirkbyacea are now assigned to the suborder Kirkbyocopina of the order Podocopida (McKenzie, Müller & Gramm in press). This recent opinion supports comments by Ishizaki (1973) that Punciidae possibly belong in Podocopida because they have podocopid-like radial and normal pore canals and a micro-ornament (both external and internal) like that of the podocopid genus *Eucytherura*. Recently, sex dimorphism has been confirmed in *P. konishii* (Nohara & Nakasone 1982). This consists of a posterior swelling in the presumed females—interpreted as a brooding space—which resembles the type of dimorphism found in numerous podocopid genera. There is no evidence of the velar, cruminal, histial or antral types of dimorphism which characterise Beyrichicopida.

The absence of a dolon (external pouch-like cavity) in punciids separates them from the homeomorphic eurychilid beyrichicopes but associates them with the other kirkbyacean families all of which likewise lack a dolon. Nevertheless, the prominent ventral frill of punciids is remarkably similar to the frill (velum) of some Beyrichicopida. Jaanusson (1957) discussed this feature in detail since he reasoned that it was highly important in classification of the order. Some further discussion seems warranted.

It is important to recognise that, "... the shell of an ostracod is merely a special part of the cuticle which is secreted by the epidermis as a continuous sheet which covers the whole surface of the body and limbs and lines both ends of the gut ..." (Harding 1964, p. 9). Ontogenetic studies indicate that the shell develops on either side of the mid-dorsum region as a fold. The two folds are initially united along the dorsal mid-line but split and separate at this mid-line zone at a later stage in embryonic development. Subsequently, each valve consists of an inner and outer lamella. The ventral border between these lamellae is the distal shell margin or flange. Calcification begins first with secretion from epidermal cells of the outer lamella; and secondarily from epidermal cells of the ventral inner lamella, proceeding from the flange inwards. As this secondary calcification continues, the marginal sensory bristles need long canals through the fused lamellae to maintain their contact with the external environment (Hartmann in Harding 1964, p. 29, 30). Detailed SEM and TEM study of podocopid pores by Okada (1982) has confirmed this functional interpretation of the marginal (radial) canals.

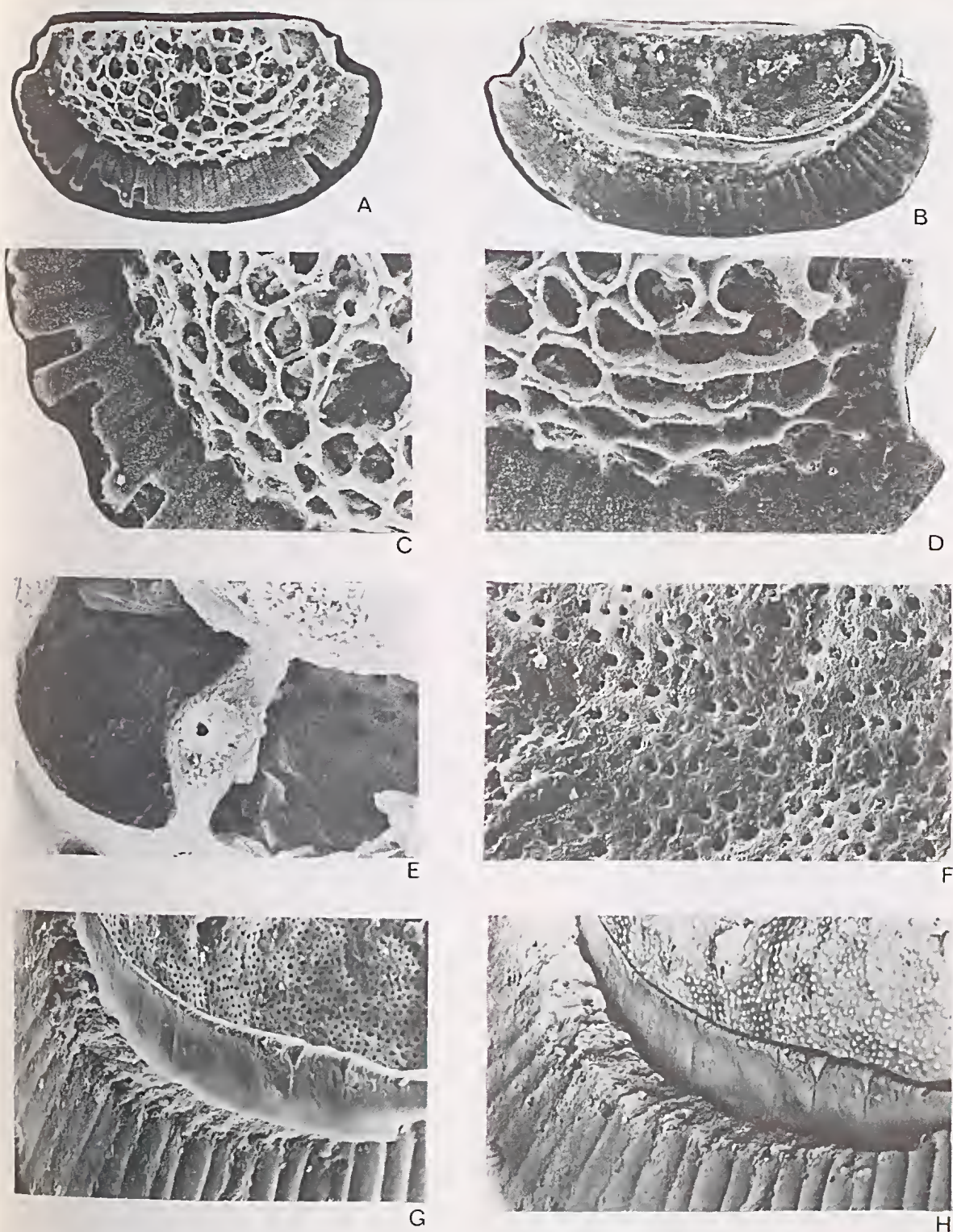
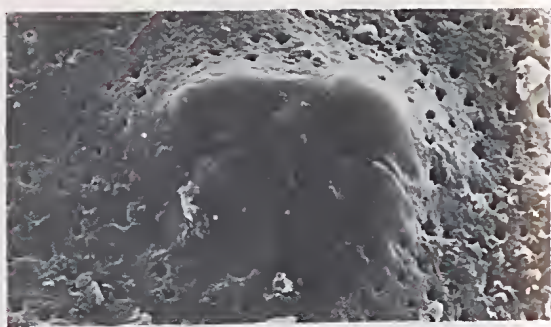


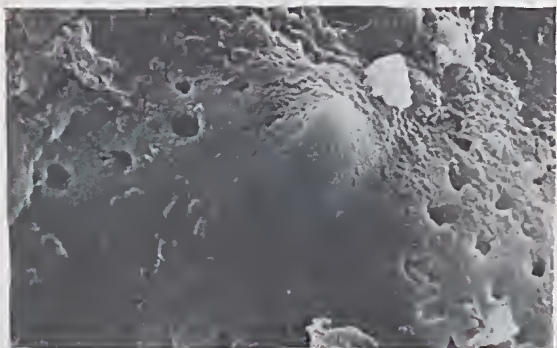
Fig. 2—*Promanawa australiensis* gen. et sp. nov. Holotype, mature male left valve (LV), NMVP74478. A, external view, $\times 154$. B, internal view, $\times 189$. C, anterioventral detail, $\times 350$. D, posteromedial detail, $\times 430$. E, detail of unrimmed and raised normal pore canal, $\times 1860$. F, detail micropunctate internal surface, $\times 1690$. G, detail posteroventral internal surface, $\times 540$. H, same as G (negative image effect created by altering the black level setting on the SEM), $\times 540$.



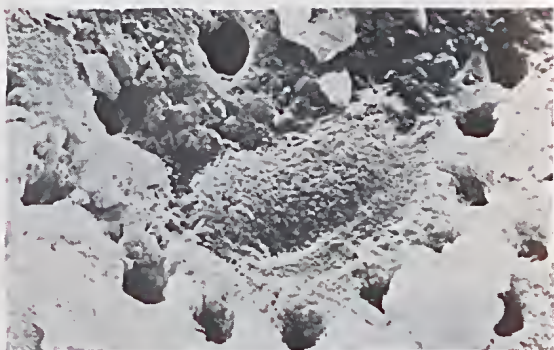
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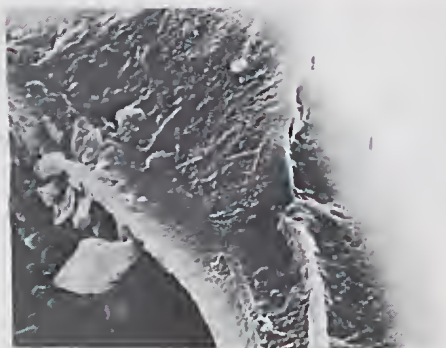
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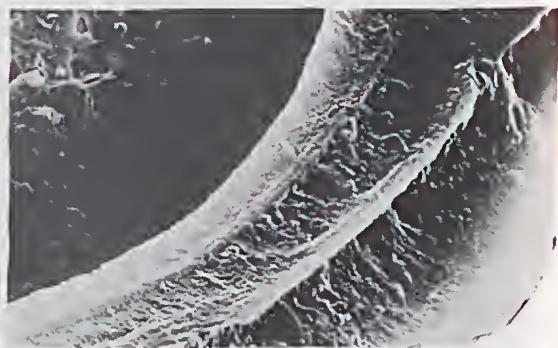
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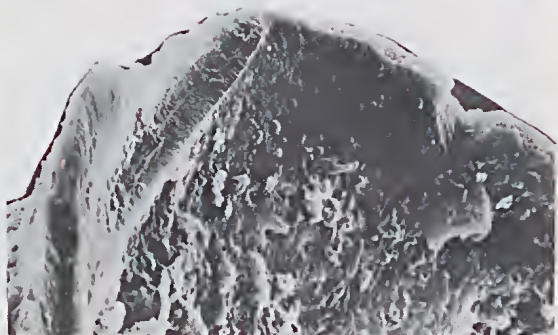
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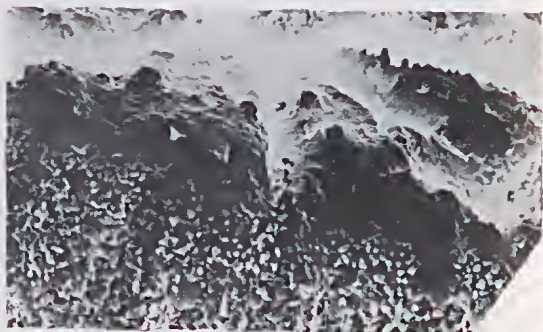
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F



G



H

The calcification of the frill clearly differs from both the primary calcification of the outer lamella and the secondarily calcified inner lamellae (Fig. 2A, B). Punciid ontogeny is virtually unknown but we suggest that the frill does not appear until relatively late perhaps not until development of the anlagen of reproductive characters in the soft anatomy.

Considered in this way, the punciid frill (velum) is a homologue of the zone of concrescence in podocopid Ostracoda and the radial 'septa' are homologues of radial pore canals. Figure 2C indicates that between these radial canals the frill is hollow. The canals extend to the edge of the selvage (Fig. 2F, G) (i.e., there are no vestibules in punciid inner lamellae). The punciid selvage is at least an analogue of the velar ridge (Jaanusson 1957) in Beyrichiocopida and might well be homologous with it.

The adductor muscle scar cluster is located slightly posterior of the midlength (Fig. 2A). This implies that the antennules and antennae of punciids are relatively elongate. The mandibular scar indicates a mandibular coxale of transverse biting type and supports a hypothesis that punciids feed benthically since mandibular scars do not occur in pelagic taxa. The more prominent dorsal muscle scar is probably the attachment site for an extrinsic muscle to the ventral rim of the antenna and the smaller dorsal muscle scar near it probably represents the attachment site of an extrinsic muscle to the dorsal rim of the antenna (Smith 1965). The size of the larger scar and its position on a well defined internal node indicate that the punciid antenna is powerful and better adapted for crawling than swimming.

Since the ventral shell margin is convex, a feature usually restricted to swimmers (e.g., Myodocopida), punciids may well be capable of some swimming bursts. However, they are unlikely to be pelagic, because the distribution of pelagic taxa is not as limited as that of punciids. Punciids probably live benthically, as other podocopids do, even such good swimmers as the cypridacean Pontocyprididae. A more likely functional interpretation of the convex ventral margin in punciids is that, along with their straight hinge line, it favours dorsal/dorsal or posterodorsal mating. The frill could also impart some stability to punciid shells thus adapting them for a benthic existence (Kesling 1969, p. 308, 309).

The distribution of Punciidae is restricted to the western Pacific, ranging from Japan to Australasia. The oldest occurrence is from the Early Miocene of New Zealand, Hornibrook (1963) having described *Puncia goodwoodensis* from the lower Goodwood Beds near Dunedin, South Island. The next oldest record is ours,

from the early Middle Miocene of Australia. The Okinawa material comes from the tuffaceous Pliocene Shinzato Formation and the Pleistocene Chinen Sand, a total of about 40 specimens having been picked thus far from washings representing 5 localities (Nohara & Nakasone 1982). Recently, new finds of Pleistocene punciids have been made in Japan by Yajima and in New Zealand by Briggs (P. De Deckker, personal communication, February 1983). Living species are confined to the warm offshore waters of New Zealand's northern Aupourian marine province where they were collected at a depth of about 175 m (Hornibrook 1949).

With such a distribution pattern, and even though the records are few, Punciidae may be considered a useful group for dating the impingement of Australasia against Indonesia according to the principles outlined by McKenzie (1978). On the punciid evidence, this event probably postdated the early Middle Miocene and antedated the mid-Pliocene, a schedule established from numerous other ostracodes (McKenzie 1978).

ACKNOWLEDGEMENTS

We acknowledge gratefully the loan of the types of *Puncia novozealandica* and *Manawa tryphena* through the courtesy of Dr. W. O. Cernohorsky, Auckland War Memorial Institute and Museum, New Zealand; and a stimulating suggestion from Dr. P. J. Jones, Bureau of Mineral Resources, Geology and Geophysics, Canberra, that the senior author consult the monograph of Jaanusson (1957). SEM micrography was carried out at the SEM unit of the Australian National University, Canberra, on a Cambridge 180 operated by Mr. John Preston. Miss Michele Fromholtz typed the manuscript. Research on the Ostracoda of southeastern Australia (K. G. M.) is supported by ARGC Grant No. E76 15127.

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Fig. 3—*Promanawa australiensis* gen. et sp. nov. Holotype, mature male left valve (LV), NMVP74478, internal views (except H). A, detail of muscle scars including central adductors, mandibular, plus 2 dorsal scars, $\times 720$. B, detail of central adductor scars, situated on internal node, $\times 1250$. C, detail of main dorsal scar, sited on internal node, plus a less prominent dorsal scar above and slightly to the right, $\times 2360$. D, detail of mandibular scar, $\times 4100$. E, detail of anterodorsal hinge accommodation groove (finely crenulate on either margin), $\times 1790$. F, continuation of E more ventrally, developing into inner list and selvage, $\times 2360$. G, detail posterodorsal terminus of hinge, $\times 1220$. H, posteroventral detail external view, showing emergence points of some pores along the inner margin of the frill, $\times 1500$.

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**WARREYUS, A NEW GENUS OF EXOEDICEROTIDAE
(CRUSTACEA, AMPHIPODA) BASED ON *EXOEDICEROS*
MACULOSUS SHEARD**

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ABSTRACT: *Exoediceros maculosus* Sheard 1936 is placed in a new genus *Warreyus* in the family Exoedicerotidae created by Barnard and Drummond (1982). A second species, *W. latrans* (Haswell 1879), is also described.

Exoediceros maculosus (Sheard 1936), an oedicerotid amphipod described from southern Australia, differs in more than 25 characters from the type species of *Exoediceros*, *E. fossor* (Stimpson 1856), and is transferred to a new genus. The new genus is assigned to the Exoedicerotidae, a family created by Barnard and Drummond (1982) for several oedicerotids in the Southern Hemisphere characterised by apical spination on the rami of uropods 1-2.

A second species, *W. latrans* (Haswell 1879), is added to *Warreyus*. It can be considered a sibling species, almost cryptic, as it differs from *W. maculosus* in several minute characters of qualitative value.

LEGENDS

Capital letters to the lower right of each figure denote the following: A, antenna; B, brood plate = oostegite; C, coxa; D, dactyl; E, epistome, left lateral; F, accessory flagellum; G, gnathopod; H, head; I, inner plate or ramus; J, incisor; K, ventral aspect of urosomite; L, labium; M, mandible; N, molar; O, palp; P, pereopod; Q, pleopod; R, uropod, S, maxilliped; T, telson; U, labrum; V, calceolus; W, pleon; X, maxilla; Y, lacinia mobilis; Z, gill. Lower case letters to the left of capital letters refer to specimens so designated in the text. Lower case letters to the right of each capital refer as follows: f, left; p, peduncle; r, right; s, setae removed.

SYSTEMATICS

Family Exoedicerotidae

Genus *Warreyus* nov.

ETYMOLOGY: Latinised masculine version of an aboriginal word meaning "to follow", in reference to the apomorphic condition of this genus relative to *Exoediceros*.

DIAGNOSIS: Body not carinate. Rostrum acute, long. Eyes paired, separate. Article 3 of peduncle of antenna 1 half or less as long as article 1. Fully articulate, scale-like accessory flagellum present. Primary flagellum of antenna 1 with articles of diverse size and armament. No articles of antenna 1 especially swollen. Mandibular incisor projecting, toothed; molar of moderate size, triturative; palp 3-articulate, article 2 straight, article 3

falciform. Inner lobes of lower lip distinct, separate, fleshy. Plates of maxilla 2 similar in size and shape, outer plate lacking thick spines. Coxae setose in part though setae short, coxa 1 ventrally truncate, coxae 3-4 rounded below, coxa 4 subrectangular, scarcely excavate posteriorly, not lobate. Gnathopods alike in both sexes, subchelate; wrists weakly lobate, not guarding hands; palms oblique, hands lacking dense fields of spines near apex of closed dactyl. Dactyls of pereopods 3-4 (and 5-6) obsolescent. Gill on coxa 5 large. Article 2 of pereopod 7 expanded and lobate. Uropod 2 not reaching far along uropod 3; peduncle of uropod 3 long, with small marginal spines, rami long. Telson entire.

TYPE SPECIES: *Exoediceros maculosus* Sheard 1936.

COMPOSITION: *Oedicerus* (sic) *latrans* Haswell 1879.

RELATIONSHIP: The two species of *Warreyus* here described differ from *Exoediceros fossor* (the only known species in the genus *Exoediceros*) in a number of different characters of which the following are considered to be of generic value: 1, the diverse size of articles and armaments on the primary flagellum of antenna 1. 2, the similarity of gnathopods 1 and 2 in both sexes and lack of gnathopodal sexual dimorphism. 3, the ordinary size of the gill on pereopod 5 (which, in *E. fossor*, is minute). 4, the subequal plates of maxilla 2 (in *E. fossor* distinctly different in size and shape). 5, the presence, on the hands of the gnathopods, of 3 or 4 rows of sharp, thin spines in place of the uniserial fields of thick, blunt spines in *E. fossor*. 6, the shape of article 3 of the mandibular palp. 7, the long, acute rostrum. Other differences are listed below in the discussion of the relationships of *W. maculosus*.

PROBLEMS OF IDENTIFICATION: Uropod 3 falls off many preserved specimens, and the apex of pereopod 7 is often missing, but the crucial generic characters such as the long acute rostrum, plus attributes of antennae, gnathopods and mouthparts, are retained. Juveniles are striking because the coxae are so poorly armed.

The two species described are easily distinguished by the presence or absence of anterior armaments on article 6 of pereopods 5-6.

Key to the species of *Warreyus*

1. Article 6 of pereopods 5-6 with all armaments grouped together posteriorly either on face or posterior margin; dactyl, though vestigial, visible and

larger than that of next couplet *W. maculosus* (Sheard)

Article 6 of pereopods 5-6 with armaments divided into two parts, mostly posterior but anterior margin with row of strong spines and setae, dactyl obsolescent and invisible except under highest magnification *W. Latrans* (Haswell)

Warreyus maculosus (Sheard 1936)

Fig. 1

1936 *Exoedicerus maculosus* Sheard, p. 452, figs 3, 4 (part).

DIAGNOSIS: Coxae 1-4 with setae long and divided into groups, posterodorsal group composed of thick curved elements, ventral group thin and flexible; article 6 of pereopods 3-4 and 5-6 distinctive; on pereopods 3-4 some facial spines forming an anterior row, thus spines in ranks of about 3-4 and 1, on pereopods 5-6 all spines together in ranks of about 4 and 0, with no spines separated into marginal row; dactyls of pereopods 3-4 obsolescent, of pereopods 5-6 much larger and visible; lateral tooth of urosomite 1 small or obsolescent.

DESCRIPTION OF LECTOTYPE (female "a" 6.45 mm, South Australia): Uropod 3, apices of pereopod 7 and of flagella of antennae 1 and 2 missing from specimen. General body form like *Exoedicerus fossor* (Stimpson) as shown by Barnard & Drummond (1982, fig. 1); rostrum acute, elongate, reaching almost to apex of article 1 on antenna 1 but head otherwise not galeate, lateral lobes narrow and submilliform, anteroventral corner of head obtusely angled softly; eyes large, paired, each with massive pigment core but periphery ommatidia (from lateral view) unpigmented.

Antennae of medium length, 2 longer than 1, articles of flagella short and bead-like, proliferate, widened and lobed alternately only on antenna 1; peduncle of antenna 1 short, articles 2-3 successively shorter than article 1, all three sparsely spinose and setose; peduncle of antenna 2 also short, articles 4-5 subequal, article 3 short, all three sparsely spinose and setose; accessory flagellum uniarticulate, small, scale-like; main flagellum of antenna 1 with complex arrangement of calceoli, swollen articles and aesthetascs; generally beyond article 12 every third article of maximum turgidity and bearing large calceolus and aesthetasc, intervening 2 articles narrower, bearing minute calceolus and no aesthetasc; first 3 basal and articles 5, 7, 9, 12 swollen, each generally with 1 aesthetasc, aesthetascs alternating in zig-zag fashion from posterior to anterior position on medial face of apex of each article, but after article 9 pattern changing to 2 articles in sequence with anterior and middle calceolus each followed by one with posterior calceolus; thus, when 0=no calceolus, p=posterior calceolus, m=middle calceolus, a=anterior calceolus, and each number marks one article, the formula for antenna 1 of female "a" is as follows: 1-0, 2p, 3p, 4m, 5p, 6m, 7p, 8m, 9p, 10a, 11m, 12p, 13a, 14m, 15p, 16a, 17m, 18p, 19a, 20m, 21p, . . . to article 53, then broken; all articles with calceolus swollen and bearing aesthetasc except articles 12 and 33 with 2 aesthetascs; antenna 2 formula=1-0, 2a, 3a, 4a, 5a, 6a, 7p, 8a, 9a, 10p, 11a,

12a, 13p, 14a, 15a, 16p, 17a, 18a, 19p, 20a, 21a, 22p, . . . 25p, . . . 28p, . . . 54p, broken.

Calceoli generally of oedicerotid form 7 (Lincoln & Hurley 1981), but differing from those of *Exoedicerus fossor* in the much smaller size, proximal receptacle being larger than part beyond waist, both receptacular elements being complexly sculptured.

Epistome with strong angular projection anteriorly, upper lip symmetrically rounded below. Incisors toothed, oblique blade, finely and evenly dentate, separating large teeth at either end; right lacinia mobilis narrow, broadening irregularly at apex; left lacinia mobilis with 7 teeth; right and left sides each with 7 stout rakers and one rudimentary; molar not very stout, subcuboid, moderately triturative; palp of medium thickness, article 1 short, article 2 weakly expanded, strongly setose, article 3 thinly falciform, longer than article 2, setae=ADE. Lower lip like illustration of *W. latrans*. Inner plate of maxilla 1 densely setose, with 9 intact setae and 2 sockets (=probably 11 setae) widely spread on right, left inner plate missing; outer plate with 11 spines; palp moderately spinosetose, 2-articulate. Plates of maxilla 2 of medium breadth, subequal, inner with full oblique facial row of setae. Plates of maxilliped small, inner with medial margins appressed and bent orally, setose, apices each with 2 stout medial spines and one more slender, subapically (=3 spines) and several larger stiff setae more laterally; outer plates not much larger than inner, medially spinose; dactyl unguiform, with 2 small subapical accessory setules.

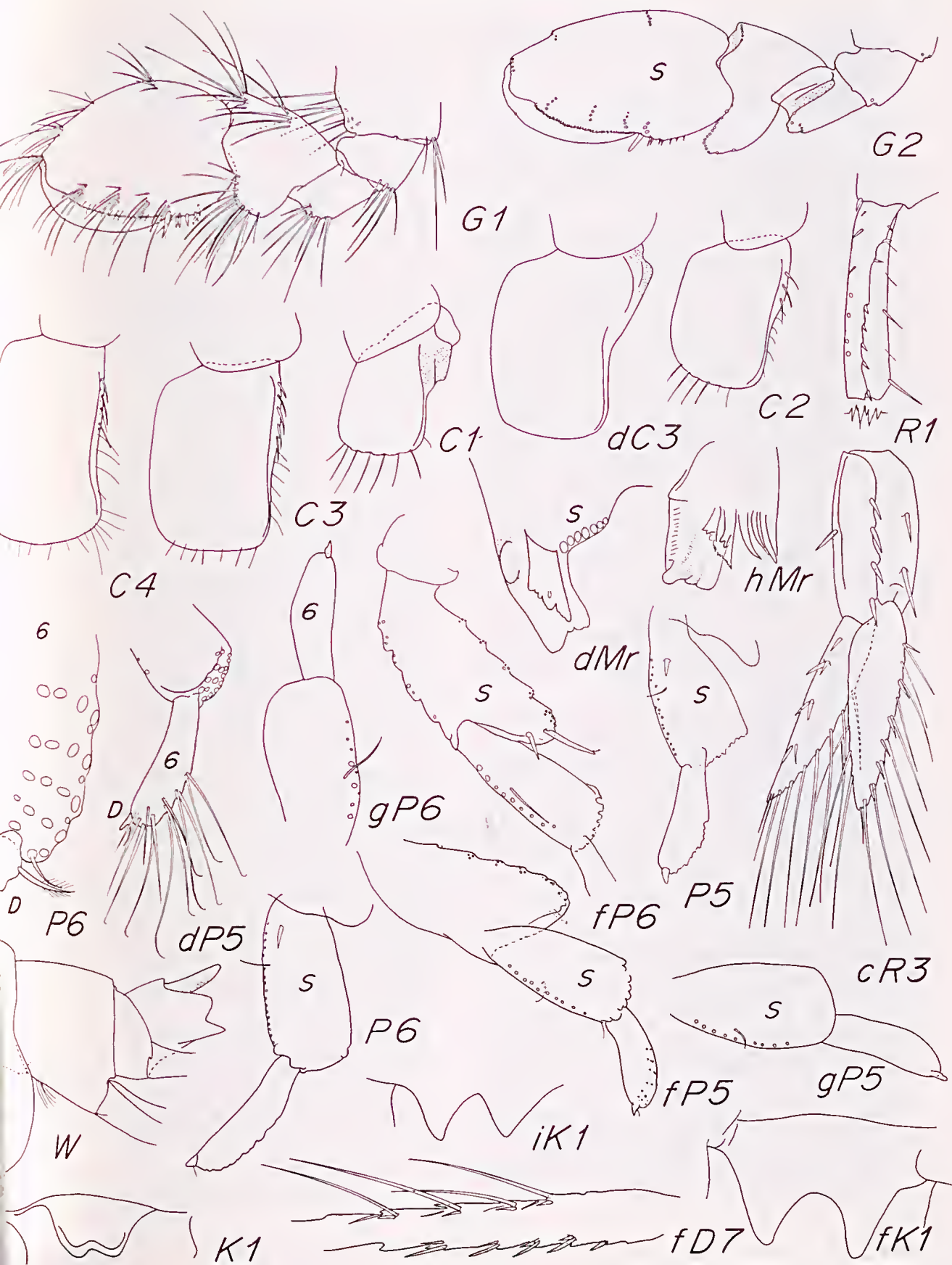
Coxa 5 scarcely shorter than coxa 4; coxa 1 truncate, with long ventral setae; coxae 2-4 all strongly setose posteriorly, proximal setae very stout; coxa 4 scarcely excavate and lobate posteriorly; coxae 5-7 with small to medium setae, setal formula of coxae=5-5-1.

Gnathopod 2 slightly larger than gnathopod 1, article 4 rather more produced and article 5 with larger lobe than in *W. latrans*, both gnathopods slightly twisted in preserved specimen.

Article 6 of pereopods 5 and 6 without anterior marginal setae, all facial setae posterior; dactyls of pereopods 3-4 vestigial, scarcely as thick as and much shorter than neighbouring spines, each dactyl with large setule; dactyls of pereopods 5-6 much larger (illustrated); article 2 of pereopods 5-6 with midfacial ridge, and of pereopods 5-7 with anterofacial ridge; article 5 of pereopods 5-6 with one basofacial spine and one facial submarginal spine-seta at about M45; dactyl of pereopod 7 unknown, broken off. Gills present on coxae 2-7, unpleated, with transverse capillaries; gills of coxae 2-5 chisel shaped, on coxae 6-7 folded and projecting medially into brood space like dried leaves. Oostegites on coxae 2-5 poorly expanded, that of coxa 5 shortest.

Pleopods more or less similar to each other, peduncles elongate, each with 2 feeble rectinacula, rami subequal but inner with fewer articles; counts of outer

Fig. 1—*Warreyus maculosus* (Sheard), unattributed drawings=lectotype, female "a"; c= male "c"; d= male "d"; f= female "f"; g= female "g"; h= female "h".



and inner rami on pleopods 1-3 = 16-17 and 14 each; peduncles of pleopods 1-3 = 0.83, 0.90 and 0.80 as long, respectively, as rami, each peduncle at base of outer ramus with free lobe bearing seta.

Epimera 1-3 each with several anterior setae; epimera 1-2 each with long facial ridge, that of epimeron 2 strongly vertical but separate spinule row placed far anterior; epimeron 1 with sparse ventral setae; epimeron 2 with posteroventral tooth and 3 pairs of ventral spinules; epimeron 3 rounded posteroventrally, ventral spine count = 1-2-2.

Urosomite 1 with weak lateral tooth above insertion of uropod 1 and broadly bifid process between rami ventrally; dorsal hump broad and weak. Urosomite 3 with weakly convex posterodorsal margin and small sharp tooth posteroventrally in mid margin between peduncles of uropod 3. Peduncle of uropod 1 with 2 lateral and 2 medial setae at ventral edges projecting to show from lateral side, lower edge with setule pits bearing spines, dorsolateral margin minutely spinulate, medial margin with 4-5 thin spines; dorsolateral margin of uropod 2 with 4 spinules, medial margin with 4 thin spines; outer rami of uropods 1 and 2 slightly shorter than inner; all rami with asymmetrical pair of apical spines and 2 others, smaller, subapically; inner rami with 2 rows of dorsal spines, outer with one row of dorsolateral spines. Uropod 3 missing. Telson very short, apex truncate and sculptured bilaterally, each of the 2 scallops bearing 2 setules; each side of dorsum with pair of setules, middle with 2 rows of denticles (both sexes).

Cuticle covered with complex pattern of fingerprint striations seen under oil immersion, groups of striations forming fields among blank spaces, striations probably under SEM composed of imbricating serrated or toothed plaques.

REMARKS: The lectotype is abnormal compared with other females examined from the same sample in: 1, smallness of the tooth on urosomite 1 above uropod 1. 2, structure of right lacinia mobilis (presumably worn). 3, presence of a basofacial spine on article 6 of pereopods 5 and 6 in addition to the submarginal facial spine-seta at about M45. 4, large size—the largest individual of *W. maculosus* in the collections, either from South Australia or from New South Wales.

MALE "d" A SYNTYPE FROM SOUTH AUSTRALIA: Very similar to female, with similar eyes, gnathopods and antennae, but minute features of antennae better developed, generally with more aesthetascs and more turgid articles. Uropod 3 missing.

Article 1 of primary flagellum on antenna 1 with 2 sets of 4 aesthetascs each, article 2 with 4, then 3 each on swollen articles 3, 5; 4 on article 8, 3 each on swollen articles 11, 14, 17; 2 each on swollen articles 20, 23, 26, 29; one each on articles 32, 35 . . . n; large calceolus on each of articles 2, 3, 4, 6, 7, 9, 10, 12, 15, 16, 18, 19, 21, 22, 24, 25, 27, 30, 31, 32, 33 . . . n; large calceolus on each of articles 5, 8, 11, 14, 17, 20, 23, 26, 29. Small calceoli in anterior and posterior positions alternatively when on adjacent articles, all large calceoli, except that on article 13 in posterior position. Right antenna 1 aberrant basal-

ly. Antenna 2 flagellum with slight alternating turgidity pattern correlated with pairs of large calceoli occurring in tandem, large calceoli occurring one each on articles 3, 5, 7, 9, 10, 12, 13, 15, 16, 18, 19, 21, 22, 24, 25, 27, 28, 30, 31; small calceolus on each of articles 1, 2, 4, 6, 8, 11, 14, 17, 20, 23, 26, 29, 32, 33, 34 . . . n; thus large calceoli of articles 12, 13, and each pair thereafter, zig-zagging slightly.

Right lacinia mobilis with 3 main and 2 subsidiary teeth and facial boss (illustrated and supplementing description of female where it was worn off).

Coxae very poorly armed, lacking posterior setae or spines, ill-developed relative to female "a", typical of smaller females and juveniles. Coxa 1 with 6 long ventral setae; coxae 2 and 3 each with anteroventral setule, no other armaments; coxa 4 with 3 posteroventral short setae; coxa 5 with 2 anteroventral setules on anterior lobe only. Setae on article 6 of pereopods 5 and 6 as in female in one posterior group only, dactyl of "enlarged" variety contrasted with *W. latrans*.

Epimeron 2 ventrofacial spine formula = 1-1-1; epimeron 3 left side = 1-1-1, right side = 1-1-1-1-1.

Uropod 3 missing.

FEMALE "b": No basofacial spine on articles 5 of pereopods 5 and 6. Epimeron 2 ventrofacial spine formula = 1-1-1; epimeron 3 = 1-1; urosomite 1 tooth as large as in *W. latrans*; outer face of peduncle on uropod 1 without basal spines.

MALE "d": No basofacial spine on article 5 of pereopods 5 and 6. Epimeron 2 ventrofacial spine formulae = 1-1-1; epimeron 3 = 1-1-1-1; uropod 3 illustrated, spine count on lateral margin of outer ramus = 1-2-2-2.

MALE "e": 2.08 mm, example also of small specimens; article 6 of pereopods 5-6 with only a few apicoposterior setae and no basofacial spine on article 5, dactyl of "large" form for *maculosus*; ventrofacial spine formula on epimeron 2 = 1-1, on epimeron 3 = 0-0-1.

FEMALE "f" 5.41 mm, OVIGEROUS FEMALE FROM TYPE LOCALITY: Article 5 of pereopods 5-6 with no basofacial spine, submarginal facial spine-seta longer on pereopod 6 than pereopod 5; inner plate of maxilla 1 bearing 11 setae; ventrofacial spine formula for epimeron 2 = 1-1-2-2; for epimeron 3 = 1-2-1-1.

LECTOTYPE: South Australian Museum C2105, female "a" 6.45 mm (newly designated and measured by us), formerly cotype. No holotype or other cotype found in Museum or elsewhere (courtesy of Dr. W. Zeidler). Illustrated herein, missing from specimen: apices of flagella on antennae; apices of pereopod 7; uropod 3. TYPE LOCALITY: Sellicks Beach, South Australia, 1936 coll. H. H. Hale.

OTHER MATERIAL: South Australian Museum C2109, syntypes from type-locality, female "b" 4.84; male "c" 4.44 mm (illustrated uropod 3); male "d" 4.85 mm; male "e" 2.08 mm; ovigerous female "f" 5.41 mm. National Museum of Victoria material, Port Jackson, New South Wales protected beach near Manly ferry wharf, coll. Dr.

Fig. 2—*Warreyus latrans* (Haswell), unattributed drawings = female "q"; i = female "i"; j = female "j".



D. M. Dexter 5 September 1980; 32 specimens, small, but with ovigerous females; female "i" 4.83 mm and subadult female "h" 4.3 mm illustrated. Eddystone Point, Tasmania, coll. Diane Higgins, April 1978, 5 specimens, female "g" illustrated.

RELATIONSHIP: Besides the generic characters cited above, *W. maculosus* differs from *E. fossor* in the following ways: 1, the acute and much longer rostrum. 2, short articles 2-3 of antenna 1. 3, slightly different calceoli. 4, broader inner lobes of lower lip (forcing stronger gape) and blunter mandibular lobes. 5, sparser setae on the inner plate of maxilla 1. 6, smaller maxillipedal plates. 7, truncate coxa 1. 8, the flatter, smoother blade of the incisor, not grossly toothed. 9, larger hands and shorter wrists (particularly in the female) of gnathopods. 10, thinner fifth article of pereopod 3-4, longer and thinner sixth article 2. 11, presence of long fine spine-setae on dactyl of pereopod 7 in addition to clumps of spines. 12, lack of lateral armaments on facial ridge of epimeron 1. 13, larger epimeron 2. 14, presence of tooth on epimeron 2. 15, presence of ventral spines on epimeron 3. 16, larger and apically bifid process on the posteroventral margin of urosomite 1 between peduncles, compared with the minute simple ovoid of *E. fossor*. 17, presence of dorsolateral spine row on peduncle of uropod 1. 18, shortness of outer rami on uropods 1 and 2. 19, stronger spination on uropods 1-2 and presence of second row of spines on inner rami. 20, greater length of uropod 3 relative to urosomite 3 and of its rami relative to peduncle. 21, presence of numerous outer spines on rami of uropod 3. 22, sculptured apex of telson.

DISTRIBUTION: South Australia to New South Wales, semi-protected and wave-beaten beaches, in sand.

Warreyus latrans (Haswell 1879)

Figs 2-4

1897 *Oedicerus latrans* Haswell p. 324, pl. 19, fig. 1.

DIAGNOSIS: Coxae 2-4 with ventral and posterior setae short and not divided into groups based on size; article 6 of pereopods 3-4 and 5-6 alike, facial spines in ranks of about 3 and 1, with row of single spines occurring on one margin in both sets of pereopods; dactyls of pereopods 3-6 alike, obsolescent; ventral tooth on urosomite 3 not vestigial.

DESCRIPTION OF FEMALE "q": 5.81 mm, New South Wales. General body form like *Exoedicerus fossor* (Stimpson) as shown by Barnard & Drummond (1982, p. 610, fig. 1); rostrum elongate, reaching almost to apex of article 1 on antenna 1 but head otherwise not galeate, lateral lobes narrow and submammilliform, anteroventral corner of head obtusely angled softly; eyes paired and large, each with massive pigment core and barely 1 or 2 rows of peripheral ommatidia (from lateral view) unpigmented. Antennae of medium length, 2 longer than 1, articles of flagella short and bead-like, proliferate, widened and lobed alternately only on antenna 1; peduncle of antenna 1 short, articles 2-3 successively much shorter than article 1, all three articles sparsely spinose and setose; peduncle of antenna 2 also short, ar-

ticles 4-5 subequal, article 3 short, all three sparsely spinose and setose; accessory flagellum unarticulate, small, scale-like; main flagellum of antenna 1 with complex arrangement of calceoli, swollen articles and aesthetascs, generally beyond article 12 every third article of maximum turgidity and bearing large calceolus and 1 or 2 aesthetascs, intervening 2 articles narrower, each bearing smaller calceolus and no aesthetascs; first four basal and articles 7, 9, 11 swollen, each swollen article generally with 2 aesthetascs, article 3—n each with calceolus (see formula for male "g" to follow, as undamaged example); flagellum of antenna 2 longer, thinner, no articles swollen, aesthetascs absent; except for article 1 each following article with small calceolus, after article 5 these calceoli alternating in zig-zag fashion from posterior to anterior position on medial face of apex of each article, but after article 16 pattern changing to 2 articles in sequence with anterior calceolus each followed by one with posterior calceolus, after article 26, pattern of 4 articles in row with calceoli gradually progressing from anterior to posterior position; formula for female "q" (using the symbols used for *W. maculosus*) as follows: 1-0, 2p, 3p, 4p, 5p, 6a, 7p, 8a, 9p, 10a, 11p, 12a, 13p, 14-0, 15a, 16p, 17a, 18a, 19p, 20a, 21a, 22p, 23a, 24a, 25p, 26-29 from a to p gradually, and following groups the same, 30-33, 34-37, 38-41, 42-45, 46-49, 50-53, 54-57, then broken after article 60.

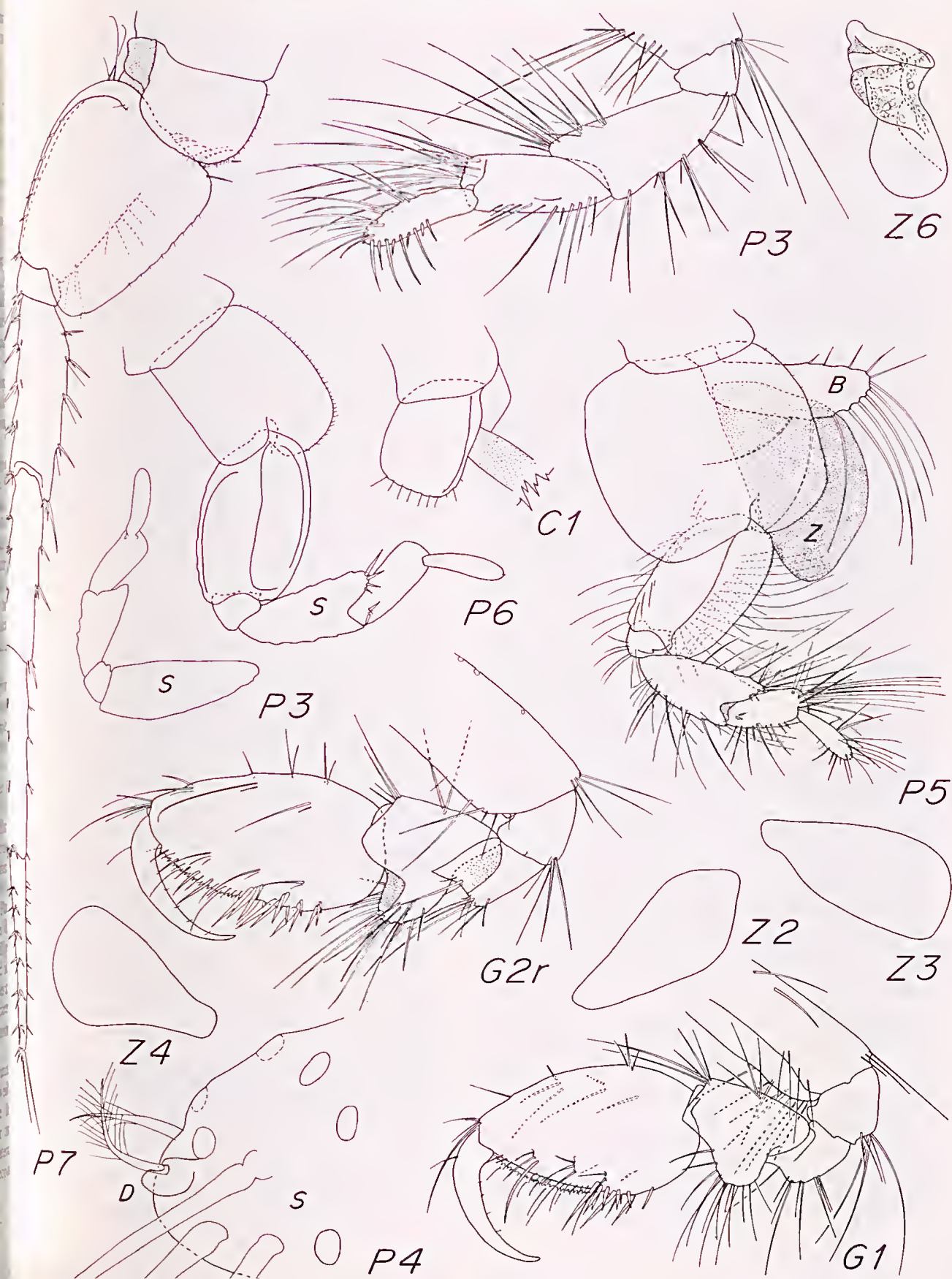
Calceoli generally of oedicerotid form 7 (Lincoln & Hurley 1981) but differing from those of *Exoedicerus fossor* in much smaller size, proximal receptacle being larger than part beyond waist, both receptacular elements being complexly sculptured, and proximal cup being larger relative to distal element.

Epistome with strong angular projection anteriorly, upper lip symmetrically rounded below. Incisors toothed, blade even, oblique; right lacinia mobilis complexly cuspidate and denticulate, left with 7 teeth; rakers stout, each side with 7 and 1 rudimentary; molar not very stout, subcuboid, moderately tritritative; palp of medium thickness, article 1 short, article 2 weakly expanded, strongly setose, article 3 thinly falciform, longer than article 2, setae = ADE. Lower lip illustrated. Inner plate of maxilla 1 with 6 widely spread medial setae, but plate not densely setose; outer plate with 11 spines; palp moderately spinosetose, 2-articulate. Plates of maxilla 2 of medium breadth, subequal, inner with full oblique facial row of setae. Plates of maxilliped small, inner with medial margins appressed and bent orally, setose, apices each with 2 stout medial spines and several larger more lateral stiff setae; outer plate scarcely larger than inner, medially spinose; dactyl unguiform with 2 small subapical accessory setules.

Coxa 5 scarcely shorter than coxa 4. Coxa 1 truncate and setose ventrally; coxae 2-7 each strongly to weakly setose posteriorly; coxa 4 scarcely excavate and posteriorly lobate. Gnathopod 2 slightly larger than gnathopod 1, both slightly twisted in preserved material.

Setae on article 6 of pereopods 5-6 like pereopods

Fig. 3—*Warreyus latrans* (Haswell), female "q".



3-4, divided into two groups of ranks in 3-1 order. Dactyls of pereopods 3-6 vestigial, scarcely as thick as, and much shorter than neighbouring spines, each dactyl with large setule. Article 2 of pereopods 5-6 with midfacial ridge, and of pereopods 5-7 with anterofacial ridge; article 5 of pereopods 5-6 with 2 basofacial spines and submarginal facial spine-seta at about M45, that of pereopod 6 longer than that of pereopod 5. Dactyl of pereopod 7 well developed, with marginal triads of spines; middle element of each posterior triad a spine-seta, much finer and longer than the other two; apex with a few medium setae.

Gills present on coxae 2-7, flat, unpleated, with transverse capillaries, gills of coxae 2-5 chisel-shaped, of 6-7 folded and projecting medially into brood space like dried leaves. Oostegites on coxae 2-5 poorly expanded, that of coxa 5 shortest.

Pleopods similar to each other, peduncles elongate, each with 2 feeble rectinacula; rami subequal but inner with fewer articles, counts of outer and inner rami on pleopods 1-3 = 18 and 15 each; peduncles of pleopods 1-3 = 0.98, 0.90 and 0.70 as long as rami respectively; each peduncle at base of outer ramus with free lobe bearing seta. Epimera 1-3 each with several setae; epimera 1-2 each with long facial ridge, that of epimeron 2 strongly vertical but separate spinule row placed far anterior; epimeron 1 with sparse ventral setae, epimeron 2 with posteroventral tooth and 3 pairs of ventral spinules, epimeron 3 rounded quadrate posteroventrally, ventral spinules = 1-2-2-2.

Urosomite 1 with weak crescentic tooth above insertion of peduncle on uropod 1, bifid tooth between peduncles ventrally, dorsal hump broad and weak; urosomite 3 with tooth on mid posteroventral margin between peduncles of uropod 3, posterodorsal margin broadly and shallowly convex above base of telson, peduncle of uropod 1 with 3 medial setae projecting to show from lateral view, lower edge with setule pits, dorsolateral margin minutely spinulate, medial margin with 5-6 thin spines; dorsolateral margin of peduncle on uropod 2 with 5 spinules, medial margin with 4 thin spines; outer rami of uropods 1-2 slightly shorter than inner, all rami with asymmetrical pair of apical spines and 2 subapical; inner rami with 2 rows of dorsal spines, outer with one row of dorsolateral spines. Peduncle of uropod 3 elongate (see figure for spine arrangement); rami broadly lanceolate, alike, medial margins strongly setose; lateral margin of inner ramus setose, outer margin of outer ramus and inner margin of inner ramus spinose; formula for outer left ramus = 1-1-2-2-2-2, for right = 2-2-2-2-2-2. Telson very short, apex truncate and bilaterally sculptured, with 2 scallops each bearing 2 setules, each side of dorsum with pair of setules, middle with 2 rows of denticles (present on both sexes, though often sparse).

Cuticle with complex pattern of fingerprint striations (seen with oil immersion), groups of striations forming fields among blank spaces, striations probably composed of imbricating serrated or toothed plaques (when seen under SEM).

FEMALE "i" (5.25 mm, ovigerous): Generally like female "q" but epimeron 3 ventral spine formula = 1-2-2 (only); lateral spines on outer ramus of uropod 3 = 1-2-2-2-2-2. Aesthetascs on primary flagellum of antenna 1, article 1 = 2 + 1, then 2 each on articles 2, 4, 8, 12, 22, then one each on articles 3, 6, 10, 15, 18, 25, 28, 32, 35, 38, 41 (43 broken); calceoli m on articles 5, 7, 9, 11, 13, 16, 19, 23, 26, 29, 33, 36, 39, 42 (broken); p on articles 2, 3, 4, 6, 8, 10, 12, 14, 15, 17, 18, 20, 21, 22, 24, 25, 27, 28, 30, 31, 32, 34, 35, 37, 38, 40, 41 (broken); swollen articles = 2, 3, 4, 6, 8, 10, 12, 15, 18, 22, 25, 28, 32, 35, 38, 41 (broken).

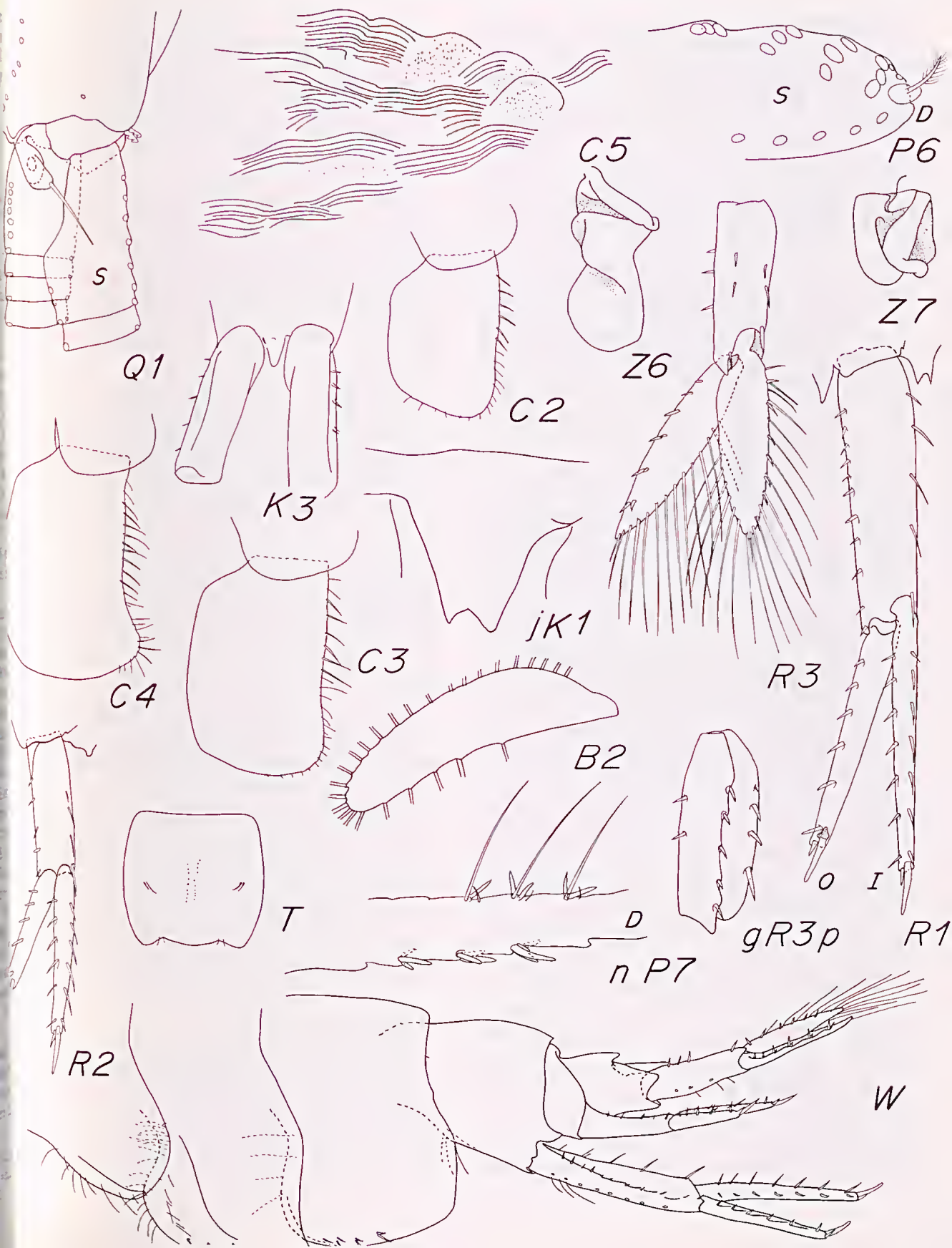
MÅLE "g" (5.79 mm): Very similar to female, with similar eyes, gnathopods, antennae and uropods, but minute features of antenna better developed, generally with more aesthetascs and more turgid articles; peduncle and uropod 3 more spinose. Article 1 of primary flagellum on antenna 1 with 2 sets of 4 aesthetascs each, articles 2-5 each with 4, then 3-4 each on swollen articles 6, 8, 10, 12, 15, 18, 21 . . . ; large calceolus on each of articles 4, 5, 6, 8, 10, 12, 14, 15, 18, 21 . . . ; small calceolus on all other articles from and including article 7. Antenna 2 flagellum with slight alternating turgidity pattern correlated with enlarged aesthetascs generally on articles 5, 7, 9, 12, 15, 18, 22, 26, 29, 33, 36, 39, 41, 44, 48, but turgidity not well correlated after article 39; small aesthetascs on articles 2, 3, 4, 6, 8, 9, 11, 13, 14, 16, 17, 19, 20, 21, 23, 24, 25, 27, 28, 31, 32, 35, etc.

TYPE LOCALITY: Bondi Beach, New South Wales, intertidal surf zone.

OTHER MATERIAL: NMVJ3798-3810—Pambula, New South Wales, 7 December 1978, collected by M. M. Drummond, female "q" 5.81 mm (illus.), female "i" 5.25 mm (aesthetascs illustrated) female "j" 6.76 mm + 33 other specimens. Mallacoota, Victoria, intertidal surf zone, 9 December 1978, coll. M. M. D. Male "g" 5.79 mm (illustrated) + 38 other specimens. Lakes Entrance, Victoria, intertidal surf zone, 10 December 1978, coll. M. M. D. 28 specimens (smallest male 4.0 mm). WPBES stations 1714, 1715, Western Entrance, Western Port, 5 specimens. Kilcunda Beach, near San Remo, Victoria, intertidal surf zone, 16 September 1976, coll. Dr. J. K. Lowry and Dr. G. C. B. Poore, 50+ specimens (largest male, 9.5 mm). Woolamai Beach, Phillip Island, Victoria, intertidal surf zone, coll. J. K. L. and G. C. B. P., 16 September, 1976, 63 specimens, male "n" (illustrated). Waratah Bay, Victoria, intertidal surf zone, 30 October, 1976, coll. G. C. B. P., 200+ specimens, male "k" illustrated. In sand on beach east of Burying Ground Point, Southport, Tasmania, coll. T. M. Walker, 20 October, 1976, 30 specimens.

REMARKS: There must be some element of doubt in the positive identification of any taxon with a species of which the original material, including types, cannot be found. The *Warreyus* species described here closely

Fig. 4—*Warreyus latrans* (Haswell), unattributed drawings = female "q"; g = male "g"; j = female "j"; n = male "n"; CS = cuticle of coxa 5, highly magnified.



resembles Haswell's *O. latrans* as far as one can judge (as far as it is possible to tell) from the original short description and meagre illustrations, except for the fact that in Haswell's figure (1879, fig. 1g) of gnathopod 2 the wrist appears shorter and broader than in our material. However, Dr. J. K. Lowry of The Australian Museum informs us that the extensive survey by Dr. Deborah Dexter of a series of beach sites in New South Wales, including sites close to the type locality of *O. latrans*, provides an adequate basis for predicting that no further species resembling *latrans* could be expected to be found there; and that it may be safely assumed that the material described here belongs to that species.

Dr. Dexter's collection became available to us after completion of this manuscript, and specimens from it which we have seen from various exposed beach sites as far north as Seal Rocks (mid-coastal New South Wales), and the single male specimen lately collected at the type locality by Dr. Lowry, appear to be identical with those described here from Victoria and southern New South Wales. A neotype should be erected after systematic study of fresh material from Haswell's type locality. It is outside the scope of this paper.

RELATIONSHIP: It differs from *W. maculosus* in the similarity of articles 6 and 7 of the two groups of pereopods 3-4 and 5-6. In *W. latrans* the facial spines on article 6 of pereopods 3-6 are divided into 2 groups in ranks of about 3-1, the rank of 1 forming a marginal row; and the dactyl of pereopods 3-6 is obsolescent; in *W. maculosus* articles 6-7 of pereopods 3-4 are like those of *W. latrans*, but on pereopods 5-6 the dactyls (article 7) are much larger, and the spines on article 6 are arranged in one facial rank with no separate marginal row; the formula thus being cited as 4-0. Further differences from *W. maculosus* are to be found in: the larger posteroventral tooth on urosomite 3 between the peduncles of uropod 3; the two stout basofacial spines on article 5 of pereopods 5-6 compared with the single spine in the lectotype and the absence of spines in other specimens of *W. maculosus* examined; the presence of an anterior group of setae on the wrist of *W. latrans* though the wrist itself is less well developed than that of *W. maculosus*; the shape of the posteroventral bifid process separating the uropodal peduncles on urosomite 1, tall and shallowly bifid in *W. latrans* short and broadly bifid in *W. maculosus*; shape of the inner plate of maxilla 1 (much rounder in *W. latrans*) and the fewer setae borne upon it—usually 5-7 in spite of its larger size, compared with the eleven most commonly present on *W. maculosus*. In both species female coxae are much more setose than those of the male, in which they are frequently reduced to one or two, or are absent altogether; and the density of setation in the females themselves from the same sample varies dramatically with the size (presumably the stage of development?) of individuals of both species so that comparison of the two in respect of setosity of coxae is not feasible.

DISTRIBUTION: Exposed ocean beaches from south-eastern Victoria to midcoastal New South Wales, sand.

NOTE ON A POSSIBLE NEW SPECIES OF *WARREYUS*

Differences between populations of *W. latrans* from different localities in respect to numbers of setae and spines, subtle variations in conformation of coxae, pereopodal articles and epimera are considered insufficient to warrant specific differentiation. Frequently they are related to body size, which varies so much from one locality to another.

However, three small specimens (one male, one subadult male and one subadult female) from Western Port (WPBES stations 1714 and 1715) resemble *W. maculosus* in the absence of anterior setae on the wrist of gnathopod 2, but resemble *W. latrans* in the presence of both anterior and posterior setae on article 6 of pereopods 5 and 6. The rostrum is longer than that of either *W. maculosus* or *W. latrans*, and the pincer-like apex of the ventral tooth on the first urosome is distinctive.

At the time of examination, evidence from these three rather poor specimens was considered inadequate to supply a firm basis for the establishment of a separate species, but samples just to hand from Werribee (Port Phillip Bay) appear to be identical with them and further investigation may confirm a third species of *Warreyus*.

Exoedicerus fossor (Stimpson 1856)

Fig. 5

1856 *Oedicerus fossor* Stimpson, p. 349.

1879 *Oedicerus arenicola* Haswell, p. 325, pl. 24, fig. 3.

1906 *Exoedicerus fossor* (Stimpson); Stebbing, p. 239.

1982 *Exoedicerus fossor* (Stimpson); Barnard & Drummond, p. 611, figs 1-5.

REMARKS: Barnard & Drummond (1982) listed many differences between *Exoedicerus fossor* and *Warreyus maculosus*, and assigned *maculosus* to the genus *Exoedicerus*, but further examination of *maculosus* and study of *latrans* confirm the generic discontinuity of *Exoedicerus* and *Warreyus*. In Fig. 5, some additional, more detailed illustrations are given of *E. fossor*: 1, highly magnified details of incisors (I) and laciniae mobiles (Y) which may be compared with similar views for the two species of *Warreyus* in Fig. 1, hMr and dMr. 2, views of the dactyl on pereopod 7(D) show lack of setae, cf *Warreyus* Fig. 2 fD7 and Fig. 4 nP7. 3, a ventral view of the posterior margin of urosomite 1 (xKl) illustrates the small size of the ovoid projection between the uropodal peduncles compared with the much larger and more elaborately shaped structures in *Warreyus* as shown in Figs 1 fKl, iKl, Kl and 4 jKl.

ACKNOWLEDGEMENTS

We thank Dr. W. Zeidler of the South Australian Museum for making it possible for us to borrow the syntypes of *Exoedicerus maculosus* Sheard, and very much appreciate his efforts to locate the holotype. We are grateful to other colleagues who contributed material used in the study: Dr. J. K. Lowry and Dr. P. Hutchings, The Australian Museum; Dr. G. C. B. Poore,



Fig. 5—*Exoediceros fossor* (Stimpson), q = male "q"; u = male "u"; x = female "x"; y = male "y".

National Museum of Victoria; Emeritus Professor J. H. Day, South Africa; Dr. Deborah M. Dexter, University of California at San Diego; Dr. J. D. Kudenov, formerly of the Marine Studies Group, Dr. T. M. Walker, University of Tasmania; Diane Hoggins and Peter Last, Tasmanian Fisheries Development Authority. Our drawings were inked by Deborah R. Fehr, and we thank Janice Clark and Wendy Brown of the Smithsonian Institution for their help.

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SILURIAN AND DEVONIAN BIOSTRATIGRAPHY OF THE MELBOURNE TROUGH, VICTORIA

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ABSTRACT: The biostratigraphy of the Silurian and Early Devonian of the Melbourne Trough is reviewed. A zonal scheme based on brachiopod assemblages is proposed, and includes the *Aegiria thomasi* Zone (early to mid Ludlow), *Notoparmella plentiensis* Zone (mid Ludlow to Pridoli), *Boucotia janaea* Zone (Lochkov), *Boucotia australis* Zone ('late' Lochkov to 'early' Pragian), and *Boucotia loyolensis* Zone ('early' to 'late' Pragian). These zones are correlated with established graptolite, conodont and dactyloconarid zones. The Siluro-Devonian boundary in southeastern Australia is based on shelly assemblages and is recognised by the abrupt appearance of the brachiopods *Schizophoria*, *Cymostrophia*, *Boucotia*, *Cyrtina* and *Cyrtinaella*.

The Melbourne Trough (Packham 1960; Fig. 1 herein) is a structural basin in the southwestern portion of the Lachlan Fold Belt (Cas *et al.* 1980). It contains Silurian and Lower Devonian marine rocks and is bounded by the submeridional Heathcote 'Axis' in the west and the Mt. Wellington 'Axis' in the east. The northern margin is covered by the Cainozoic Murray Basin succession; the southern margin is overlain by the Mesozoic and Cainozoic sediments of the Otway and Gippsland Basins.

A zonation of the Silurian and Devonian sequence is now possible on the basis of brachiopod faunas which may be integrated with standard graptolite and conodont zonations established elsewhere (Fig. 2, facing page 94). The zonal scheme is based on information from a large number of fossil localities within the Melbourne Trough (Garratt 1981a).

The brachiopod zonal scheme is divided into a number of assemblage zones here used in the sense of Hedberg (1976).

The Silurian and Devonian faunal zones of the Melbourne Trough are correlated with the graptolite zones of the British Silurian (Rickards 1976) and with the Upper Silurian and Lower Devonian of central Europe (Czechoslovakia and Poland) (Teller 1969, Jaeger 1959, 1979). Although much of the Victorian Upper Silurian-Lower Devonian lacks graptolites, correlation with the Bohemian stages is possible because *Monograptus aequabilis notosaequabilis* is found in Europe (Jaeger 1979) and Victoria (Jaeger *et al.* 1969). Further *M. thomasi* and the conodont *Eognathodus sulcatus sulcatus* occur in the same section in the eastern half of the Melbourne Trough and denote established Pragian zones (Jaeger 1979, Klapper & Zeigler 1979).

As yet graptolites are unknown from the Rhenish Devonian sequence and conodonts are uncommon, making it difficult to correlate with the sequence in south eastern Australia. Use of the terms Gedinian, Lochkovian, Siegenian and Pragian follows that of Lütke (1979) and Jaeger (1979), rather than that of House (1979), Johnson (1975, 1979) and Norris (1979).

PREVIOUS CORRELATION SCHEMES IN THE MELBOURNE TROUGH

Early attempts at subdividing the Silurian-Devonian of the Melbourne Trough were carried out by trying to correlate the local sequence with Murchison's (1839) Silurian series of Britain. McCoy (1874-1888) subdivided the "Upper Silurian" series (= Silurian) of central Victoria into May Hill Sandstone (oldest), Wenlock and Ludlow, and gave very brief lists on the maps of Selwyn (1854-5), Aplin (1868), Taylor (1864a,b), Aplin & Taylor (1862), and Selwyn & Aplin (1858).

Gregory (1903) nominated local series for the Silurian of Victoria. He proposed a two-fold subdivision based on the palaeontological identifications of McCoy (1874-1888) and Etheridge (1878). The Melbourne Series (older) was based on faunas from Moonee Ponds Creek, Melbourne, and the younger Yering Series was based on collections made by Selwyn, Cresswell and Sweet from Yering, north of Lilydale.

Jutson (1908) and Chapman (1908) recognised an informal unit, "the Passage Beds", between the Yeringian and Melbourne Series, for a suite of fossils from beds low in the Merriang Syncline and also included those from Jutson's "*Spirifer*" band.

Chapman (1914, p. 212) thus interposed the Tanjilian Series to his (1908) scheme based on the *Panenka* Shales of the Tanjil River, Gippsland. He provided a full fossil list for the local Silurian series including *Aegiria thomasi* with most of the fossils given by him having been reassigned to other genera by Garratt (1981a). Hall (1914) described the monograptids *Monograptus aplini* and *M. turriculatus* from Aplin's (1868) section at Keilor and correlated them with zones 22 and 23 of the British Llandovery.

Jones (1927) described *Monograptus chimaera*, *M. roemeri*, *M. colonus* and *M. varius* from Studley Park, and correlated them with Elles & Woods' (1901-1918) zone 33 of the early Ludlow of Britain.

Thomas & Keble (1933) recognised 3 local Silurian Series
3. Yarravian (youngest)

2. Yeringian

1. Keilorian (oldest)

1. The Keilorian (Llandovery) is typically exposed at Keilor. The top of the series was marked by the occurrence of *Monograptus riccartonensis*, which incidentally was misidentified by Chapman (1914, p. 222).
2. The Yeringian (Wenlock) typically exposed at Lilydale and based on age determinations of the shelly fauna by McCoy (1874-1888) and Chapman (1914).
3. Yarravian (=Melbournian) typified by the widespread distribution of zone 33 graptolites in the Melbourne area.

Gill's (1941) sequence was as follows: 1. Keilorian, 2. Melbournian, 3. Jordanian, typically exposed in the Jordan River, and including the beds of the *Panenka-Styliolina* association (=Tanjilian), 4. Yeringian (youngest).

Thomas (1960) subdivided the Silurian into four series. He introduced the name Eildonian, which he correlated with the British Wenlock. This series name was earlier used by Thomas (1947, p. 16) for the supposedly Wenlock Eildon beds. The occurrence of the late Wenlock graptolite *Monograptus testis* from Cottles Bridge was cited as indicative of the Eildonian. Thomas (1960) also recognised that the Tanjilian succeeded the Melbournian, and correlated the Tanjilian series with the Upper Ludlow of Britain.

Gill (1965) subdivided the Yeringian into a lower assemblage typified by the fauna of Ruddock's Quarry, G20 of Gill (1942) and an upper assemblage typified by the fauna at Hull Road, Lilydale (Gill, 1942). Strusz (1972) recognised four faunal associations for the Lower Devonian rocks of Victoria based on brachiopods. He accepted Gill's (1965) subdivision of the Yeringian, expanded the faunal lists and noted the possibility of a Pridolian age for the base of the Yeringian. His four faunal associations were: Lower Yeringian (Pridoli to early Pragian); Upper Yeringian (Pragian) Tabberabberan (late Pragian); Buchanian (late Pragian to Early Middle Devonian).

Talent *et al.* (1975) noted that after 1960 the names for the local Silurian series progressively fell into disrepute and the local Victorian Silurian sequence was directly correlated with the British series. Talent *et al.* (1975) recognised eleven graptolite zones in the Australasian Silurian.

BASIS FOR ZONATION OF THE SILURIAN AND DEVONIAN OF THE MELBOURNE TROUGH

No attempt is made to utilise earlier Silurian and Devonian series nomenclature for the Melbourne Trough. Identification of the Silurian graptolite zones relies on recent compilations of the British zonal scheme (Rickards 1976, Rickards *et al.* 1977), the Polish zonal scheme (Teller 1969) and the Australian scheme (Talent *et al.* 1975). Ranges of various graptolites have been shown to differ in different parts of the world during the Silurian (Churkin & Carter 1970, Rickards 1976, Teller 1969). This suggests that there are inherent problems in

intercontinental correlations based on graptolites that may be due to facies changes or diachronism. Nevertheless, the *acuminatus*, "*gregarius*", *crispus*, *testis*, *nassa* (the *dubius-nassa* interregnum) and *nilssoni* zones of the Silurian and the *uniformis* to *hercynicus* zones of the Devonian appear to be recognised world-wide and may not be time transgressive. All these zones are represented in southeastern Australia except those of the Devonian (Lochkovian) which are either rare or absent.

GRAPTOLITE ASSEMBLAGE ZONES

The graptolite assemblage zones used herein follow those of Talent *et al.* (1975). Treatment of the graptolite zones is confined to new information (i.e. post 1975), pertinent pre-1975 information not mentioned by Talent *et al.* (1975), and those graptolite zones which are important for brachiopod correlation.

The base of the Silurian is yet to be recognised in the Melbourne Trough. The contact between the Ordovician and the Silurian is either faulted, unexposed, or represented by an unfossiliferous interval (Webby 1976, Sherwin 1979, A.H.M. VandenBerg 1981 pers. comm., Richards & Singleton 1981).

ORTHOGRAPTUS cf. ACUMINATUS ASSEMBLAGE ZONE

This zone is defined by the presence of rare *Orthograptus* cf. *acuminatus* near Konagaderra northwest of Melbourne, and *Glyptograptus* cf. *persculptus* near Mt Wellington (Harris & Thomas 1954, Talent *et al.* 1975, p. 54). The zone has also been recognised in Tasmania by Baillie *et al.* (1978).

CORONAGRAPTUS GREGARIUS ASSEMBLAGE ZONE

The *gregarius* zone is present in the Jackson's Creek section at Sydenham, north west of Melbourne (Fig. 2). Thomas & Keble (1933, p. 59) and Harris & Thomas (1949) recorded an assemblage of graptolites from localities 8a and 8b (300 m above the base of the Ordovician-Silurian boundary) in Jackson's Creek as *Monograptus triangulatus fimbriatus*, *Pristiograptus concinnus*, *Glyptograptus tamariscus*, and *G. sinuatus*. To this should be added a specimen in their collection identified as *Climacograptus scalaris* s.s. by R. B. Rickards (1977, written communication) from loc. 8b. The underlying 300 m are unfossiliferous. The *gregarius* zone may also be recognised at Heathcote where Thomas (*in* Öpik 1953, p. 10) recorded *P. (M.) hughesi* and *Pristiograptus* cf. *jaculum* from the *Illiaenus* Band (Fig. 2).

MONOGRAPTUS TURRICULATUS ASSEMBLAGE ZONE

This zone may be recognised in the Jackson's Creek Section at Sydenham, where Thomas & Keble (1933, p. 60) recorded *M. sedgwickii* from the base of the Springfield Formation at loc. 7. Their material has been reidentified as *M. cf. marri* (R. B. Rickards 1977 pers. comm.). This horizon underlies strata containing an *exiguus* Zone assemblage (locs 5 and 6 of Thomas & Keble, 1933) by some 150 m (Fig. 1).

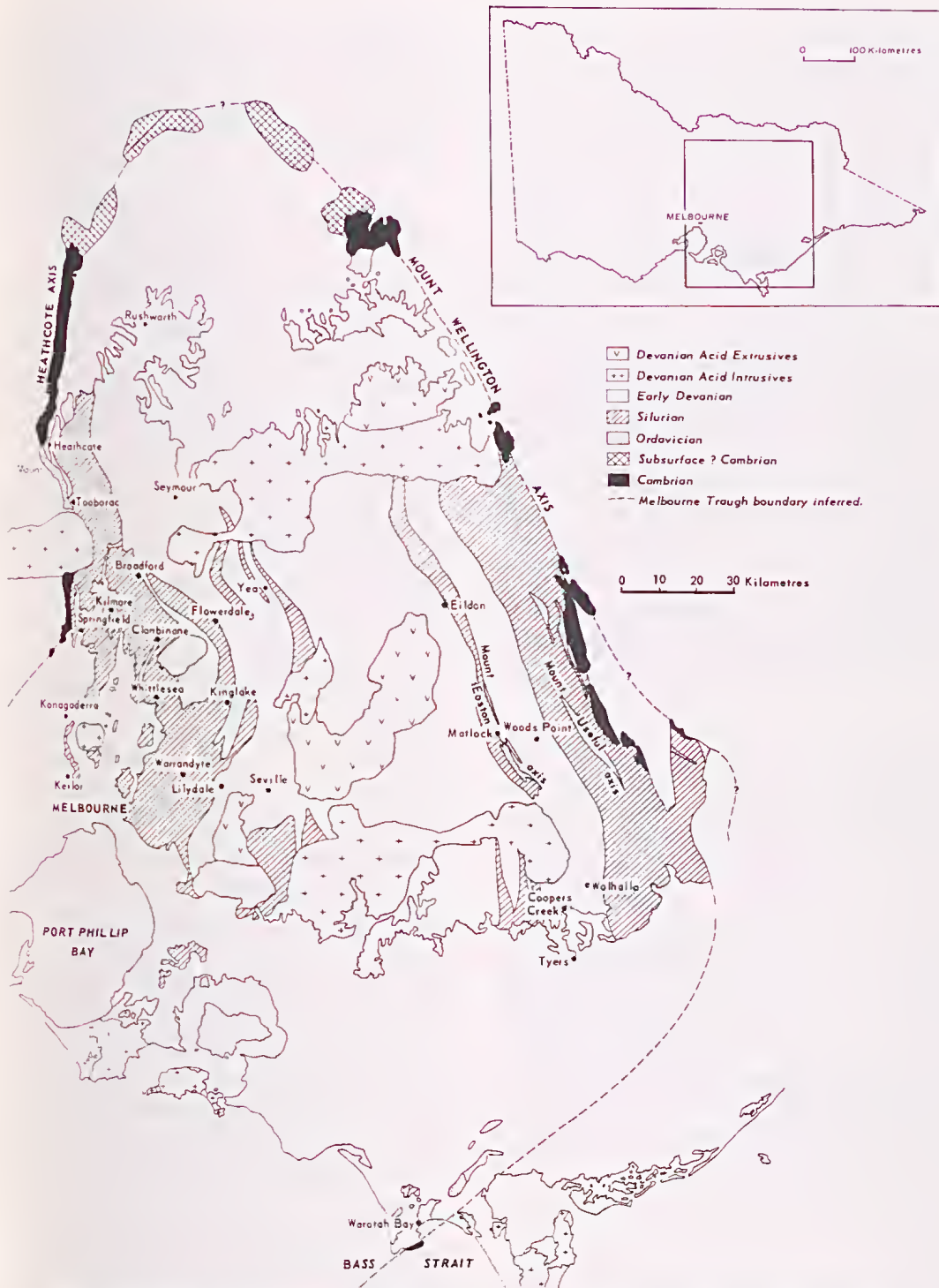


Fig. 1—Locality map of the Melbourne Trough. The Silurian is shown with oblique hatching; the Devonian as blank.

Harris & Thomas (1937, p. 73, 74) found *M. priodon* and *M. runcinatus* at two localities near the base of the Springfield Formation in No. 3 Creek, allotments 20 and 9 respectively, Parish of Springfield (Fig. 2). A *maximus* to *turriculatus* zone age is indicated.

MONOGRAPTUS EXIGUUS ASSEMBLAGE ZONE

M. exiguus is widespread in the Melbourne Trough and in New South Wales and probably corresponds to the *crispus* and *greistonensis* zones of Great Britain (Rickards 1976) as well as the *M. crispus* Zone of Sher-

rard (1954, p. 90). In Poland *M. exiguus* ranges from the *turriculatus* to *crispus* zone (Teller 1969).

The *exiguus* zone occurs 150 m above the base of the Springfield Formation (VandenBerg & Schleiger 1972) at localities 5 and 6 along Jackson's Creek (Thomas & Keble 1933, Fig. 2), where *M. crispus*, *M. rickardsi* (earlier identified as *M. halli* by Thomas & Keble 1933) (R. B. Rickards 1977 pers. comm.), *M. marri*, and *Pristiograptus nudus* are found. The zone is also known from isolated localities in the Anderson Creek Formation near Macclesfield, south of Lilydale (fauna includes *M. marri*, *M. Priodon*, and *M. cf. spiralis*, D. E. Thomas and P. R. Kenley 1968, pers. comm.) at Warrandyte (Gill 1952) and at Arthurs Creek (Garratt 1972). The *exiguus* zone is known from several localities in the McAdam Sandstone (VandenBerg 1975b) which crops out within the Mount Easton "Axis" in the eastern portion of the Melbourne Trough. Here, Keble & Harris (1934) and Harris & Thomas (1947) recorded the assemblage *M. exiguus*, *M. marri* (earlier identified as *M. pandus*), *M. spiralis*, *M. priodon*, *Retiolites geinitzianus*, (earlier identified as *Stomatograptus australis*), and ?*Rastrites*. This collection has been re-examined by R. B. Rickards (1977 written communication). In the Waratah Bay district an inlier of Silurian sandstone and shale has yielded an assemblage of *M. marri* (recorded as *M. cf. pandus*) and *Dictyonema* sp. by Douglas & Paton (1972); an assignment to the *exiguus* zone may be indicated.

TESTOGRAPTUS TESTIS ASSEMBLAGE ZONE

For the distribution of this zone in New South Wales see Talent *et al.* (1975). *T. testis* is extremely rare in the Melbourne Trough. Only one specimen has been found at Cottles Bridge approximately 900 m below the top of the Anderson Creek Formation (Garratt 1975), at loc. E9, (Fig. 2).

GOTHOGRAPTUS NASSA ASSEMBLAGE ZONE

The "*nassa-dubius* interregnum" (Jaeger 1959) is yet to be documented in Australia (Sherwin 1979, p. 160). Rickards (1976, p. 170) accords this interregnum full zonal rank in Great Britain where it is recognised in North Wales, Ludlow and Wenlock Edge, Shropshire (Holland *et al.* 1969, Bassett *et al.* 1975). Between Melbourne and Warrandyte, *Gothograptus nassa* occurs 10 m (loc. G200a) above an association of *M. flemingi*, *Pristiograptus pseudodubius* and *Pristiograptus* sp. (loc. G200) (Garratt 1975, Garratt in VandenBerg *et al.* 1976), (Figs 2 & 3). Identifications of the lower assemblage are supplied by R. B. Rickards (1977 written communication).

NEODIVERSOGRAPTUS NILSSONI ASSEMBLAGE ZONE

Sherwin (1979, p. 161) stated that 'the British zones of the early Ludlow cannot be recognised with any exactitude' (for Australia) 'but this is possibly the result of existing uncertainties in England'. Rickards (1976) earlier drew attention to these "uncertainties" and suggested that the *nilssoni* zone s.l., may in fact be differentiated into a lower *nilssoni* zone and an upper *progenitor* zone, as in Poland (Teller 1969).

The *nilssoni* zone was first recognised in Australia by Jones (1927) who described *M. chimaera*, *M. roemeri*, *M. varians* and *M. colonus*, from Studley Park, Melbourne. It is also known from Heathcote (Harris & Thomas 1937), Queenstown and Yellingbo (D. E. Thomas & P. R. Kenley 1968 pers. comm.). At Heathcote, the *nilssoni* zone occurs in the upper part of Unit 2 of the Dargile Formation (Thomas 1941a) and underlies a *scanicus* zone assemblage by 400 to 600 m (Fig. 3). Localities H33 and H41, Parish of Heathcote have yielded *Neodiversograptus* cf. *nilssoni* and *Saetograptus colonus* (Fig. 2) whilst locality H35, Parish of Heathcote, has yielded *Monograptus uncinatus* and *Pristiograptus* cf. *dubius*. Within Melbourne, the *nilssoni* zone ranges from close to the top of the Anderson Creek formation up into the Dargile Formation. At Eltham (loc. E1) and Wonga Park (loc. E2) northwest of Lilydale, *S. colonus* occurs in the upper beds of the Anderson Creek Formation (Garratt 1975) (Figs 2 & 3). At Craigieburn (loc. M1), north of Melbourne an equivalent horizon has yielded *Pristiograptus jaegeri*, *M. ludensis*, and *S. varians* (Rickards in VandenBerg *et al.* 1976, p. 48). At Studley Park (loc. M2) the assemblage described by Jones (1927) has been reidentified by Rickards (1977, written communication) as including abundant *S. incipiens* and *S. varians*, occasional *S. colonus*, and very rare *S. roemeri*, to which should be added *Lobograptus crinitus* (Harris & Thomas 1937, p. 12, Fig. 3). Localities M3, 4 and 5 within the City of Melbourne contain *S. varians*, *S. colonus*, *N. cf. nilssoni*, and *Pristiograptus dubius* (Thomas & Keble 1933, p. 76). Recent excavations during the construction of the Melbourne Underground Rail Loop have shown that structurally and stratigraphically these localities lie beneath the starfish beds of Withers & Keble (1934a, b) (e.g. M6) by approximately 50 m (J. Neilson 1978, pers. comm.). Elsewhere in the western portion of the Melbourne Trough, the starfish beds contain *S. chimaera*, a species which is indicative of the overlying *scanicus* Zone, suggesting that at least two starfish horizons occur in the early Ludlow of the Melbourne Trough.

D. E. Thomas & P. R. Kenley (1968, pers. comm.) found *N. nilssoni* and *Bohemograptus bohemicus* at Cottles Bridge (loc. M7) and this locality was shown by Garratt (1972) to be above the base of the Dargile Formation. This assemblage together with *S. cf. colonus* occurs at Yellingbo (loc. M8) east of Macclesfield (Figs 2 & 3). *S. colonus* is known from localities D140 and D143 at Whittlesea (Williams 1964, p. 283, Fig. 3a), and *Bohemograptus bohemicus* occurs at locality E3, 1.5 km east of the junction between Watson Creek Road and Panton Hill Road, Christmas Hills. These localities occur between 50 and 200 m above the base of the Dargile Formation.

SAETOGRAPTUS SCANICUS ASSEMBLAGE ZONE

At Heathcote, Harris & Thomas (1937, p. 71, pl. 1, figs 9-12) illustrated and described *S. chimaera*, *S. colonus* var. *compactus* from locality 40, Parish of Redcastle and loc. 37, Parish of Heathcote; the latter locality

also yielded *Bohemograptus bohemicus*, and *Monograptus uncinatus*. *S. chimaera* has been recorded from localities 35A and 32, Parish of Heathcote and locality 8D, Parish of Dargile (Harris & Thomas 1937, p. 72). All occur close to the top of Unit 3 of the Dargile Formation as mapped by Thomas (1941 a, b), and overlie localities containing *nilssoni* zone graptolites by 400–600 m (Fig. 3).

Williams (1964, p. 283, fig. 3g) described *Monograptus varians* var. *pumilis* from locality F31 (= Bb23 east of Kilmore) but it was later reidentified as *S. chimaera* by Jaeger (1967, p. 284). It occurs in sandstone containing starfish which are stratigraphically below the *Aegiria-Encrinurus* beds (Garratt 1977).

GRAPTOLITE OCCURRENCES BETWEEN THE *SCANICUS* AND *THOMASI* ASSEMBLAGE ZONES

In the western portion of the Melbourne Trough sporadic isolated occurrences of graptolites are known over a stratigraphic range from the upper beds of the Dargile Formation and the overlying Humevale Formation (Williams 1964, Garratt 1979). All the species so far recovered range through the Ludlow. These localities give an upper and lower age limit to the *Aegiria thomasi* and *Notoparmella plentiensis* assemblage zones respectively.

Monoclimacis cf. *haupti* and *Bohemograptus bohemicus* are known from Arthurs Creek (locality T8) (D. E. Thomas & P. R. Kenley 1968 pers. comm.) and Upper Plenty (locality F10 Williams 1964, p. 283, Fig. 3F), and are high in the Dargile Formation (Garratt 1972, 1977). They correlate with the *Aegiria-Encrinurus* mudstones (Unit 4 of the Dargile Formation); a late Ludlow age is suggested.

At Yea, two localities within the upper 40 m of the Yea Formation contain *Bohemograptus bohemicus* and *P. cf. dubius*, and *Monograptus* cf. *uncinatus uncinatus* respectively (R. B. Rickards 1980 pers. comm., Garratt 1981a, 1981b). These localities occur in the Lower Plant Assemblage (Garratt 1979, 1981b) which contains elements of the *Baragwanathia* flora (Douglas 1976 unpubl., Garratt 1979) and strongly implies a Ludlow age for the earliest *Baragwanathia* flora, perhaps as old as *scanicus* Zone. They have been correlated with the upper beds of Unit 4 of the Dargile Formation. The overlying sandstones of the Rice's Hill Sandstone Member at Yea, and the Clonbinane Sandstone Member at Broadford, Flowerdale and Whittlesea are considered coeval, although lithologically distinct (Fig. 5).

Three localities containing probable Ludlow graptolite assemblages are known from the Humevale Formation. Williams (1964, p. 283, fig. 3) illustrated a form as *Monograptus* cf. *dubius thuringicus* from loc. X50 at Reedy Creek, 100 m above the Clonbinane Sandstone Member. This specimen has been reidentified as *P. cf. haupti* by Jaeger (1977 written communication). Further east at Tunnell Hill between Flowerdale and Yea, Williams (1964) illustrated a form as *M. cf. uncinatus* from loc. E56, approximately 900 m above the Clonbinane Sandstone Member (Figs 2, 5). At loc. E10,

Strath Creek, and at approximately the same stratigraphic position as loc. E56, *B. bohemicus*, *P. dubius* and *Linograptus* sp. have been recovered (Garratt, 1979). These graptolite localities, although widely distributed suggest an upper age limit for the Clonbinane Sandstone Member, of late Ludlow. This conflicts with Schleiger's identification (*in* VandenBerg *et al.* 1976, p. 51) of the Pridoli form *M. aequabilis aequabilis* from just above the Clonbinane Sandstone Member at Coulson's Crossing, Clonbinane. Clarification of this conflict must await description of these graptolites from Coulson's Crossing.

MONOGRAPTUS THOMASI ASSEMBLAGE ZONE

The *M. thomasi* Assemblage Zone was first established in Victoria by Jaeger (1966, 1967). It is widely distributed, both vertically and laterally in the Wilson Creek Shale of the Melbourne Trough (Talent & Banks 1967, VandenBerg 1975b, VandenBerg *et al.* 1976). It is not known elsewhere in southeastern Australia, although Sherwin (1979, p. 161, 2) recorded a form as *M. aff. thomasi* in association with *M. transgrediens* from Cheeseman's Creek, New South Wales.

M. thomasi Zone has been found in Malaya (Jones 1973), Guangxi Province of China (Mu & Ni 1975, Wang 1975), Nevada, U.S.A. (Berry & Murphy 1972, Johnson 1977b), and Western Canada (Jackson *et al.* 1978, Lenz 1979, Jaeger 1979).

There is uncertainty as to whether the *thomasi* zone is 'early' or 'late' Pragian. Consideration of this problem hinges on the stratigraphic relationship between the *thomasi* zone and *sulcatus sulcatus* zone, as well as their relationship with other Pragian graptolites. Evaluation of the stratigraphic position of the *thomasi* zone in the Early Devonian of the Melbourne Trough is hampered by the absence of Lochkov graptolite zones and by the facies control of the *thomasi* zone within the Wilson Creek Shale, both the lower and upper boundaries of the *thomasi* zone are coincident with the lower and upper boundaries, respectively, of the Wilson Creek Shale. At Eildon, Matlock and Walhalla, the upper few metres of the Wilson Creek Shale contain *M. aequabilis notoaequabilis* as well as *M. thomasi*. *M. aequabilis notoaequabilis* is found in the overlying siltstones of the Norton Gully Sandstone (VandenBerg 1975b). Further west at Killingworth, near Yea, *M. thomasi* is found in a tongue of Wilson Creek Shale above the Flowerdale Sandstone Member (loc. 10 of Harris & Thomas 1942) (Couper 1965, Garratt 1979). At Seymour, *M. thomasi* occurs in two tongues of Wilson Creek Shale—the lower tongue above the Flowerdale Sandstone Member (loc. F2) and the upper tongue immediately overlying the Broadford Conglomerate Member (locs. F1, F3 and F5 of Schleiger 1964). *M. aequabilis notoaequabilis* is found in association with *M. thomasi* at loc. 1 near Seymour, and is also known from a higher tongue of the Wilson Creek Shale at loc. F4 near Sanitary Gully, east of Seymour (Schleiger 1964). Thus the graptolite succession replicates that of Matlock, but over a thicker sequence of strata (Garratt 1979, Fig. 4). At Yea,

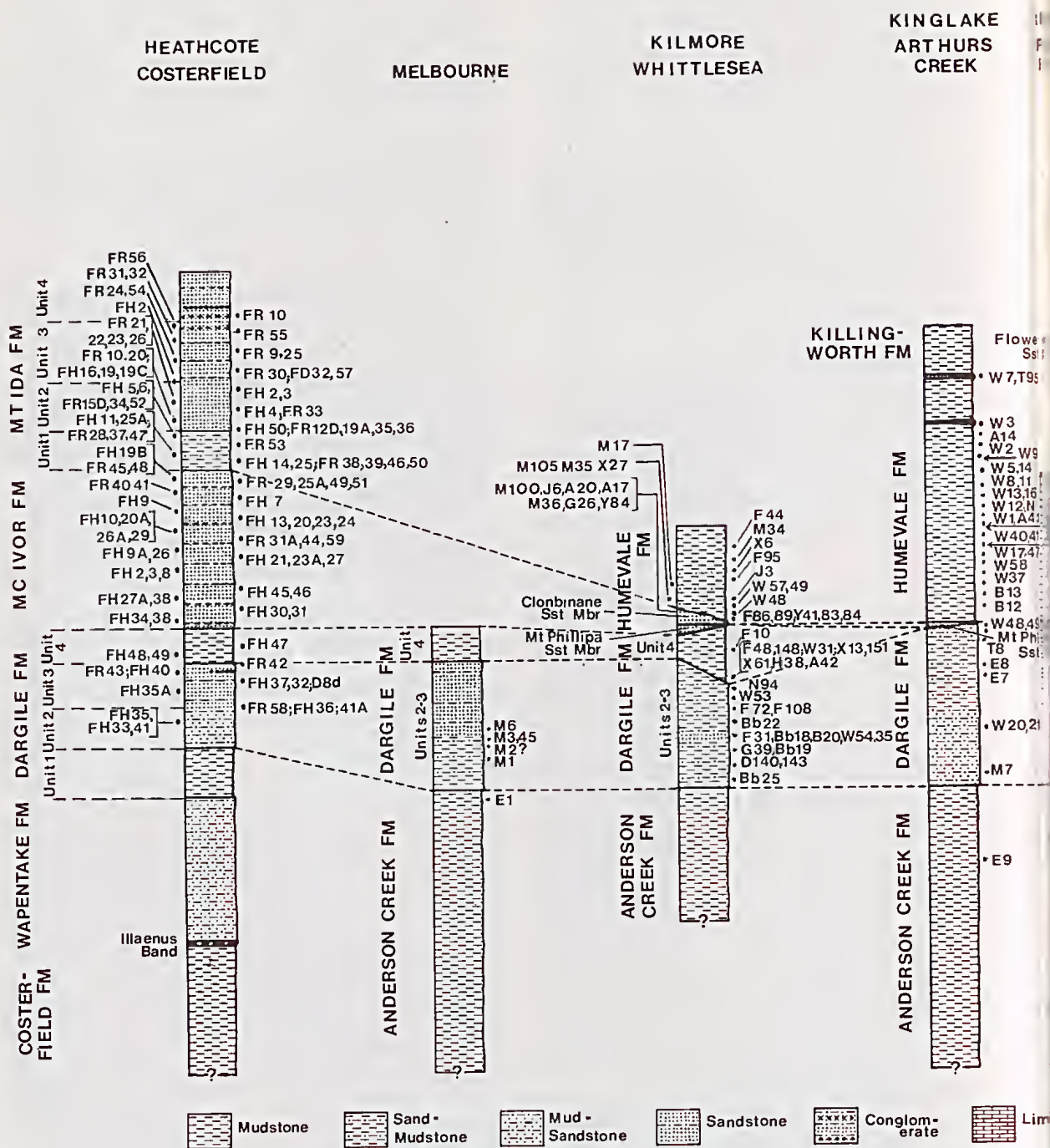


Fig. 3—Composite lithostratigraphic correlation of Silurian-Devonian of south central Victoria. Note that the fossil locality captions are published as far as Heathcote (Talent 1965a) Kilmore and Kinglake (Williams 1964), and Lilydale and Seville (Gill 1942, VandenBerg 1971). Other localities not included in the above publications are listed by Garratt (1981, unpubl.).

WARRANDYTE
CHRISTMAS
HILLS

LILYDALE
CROYDON

SEVILLE
MACCLESFIELD

EILDON

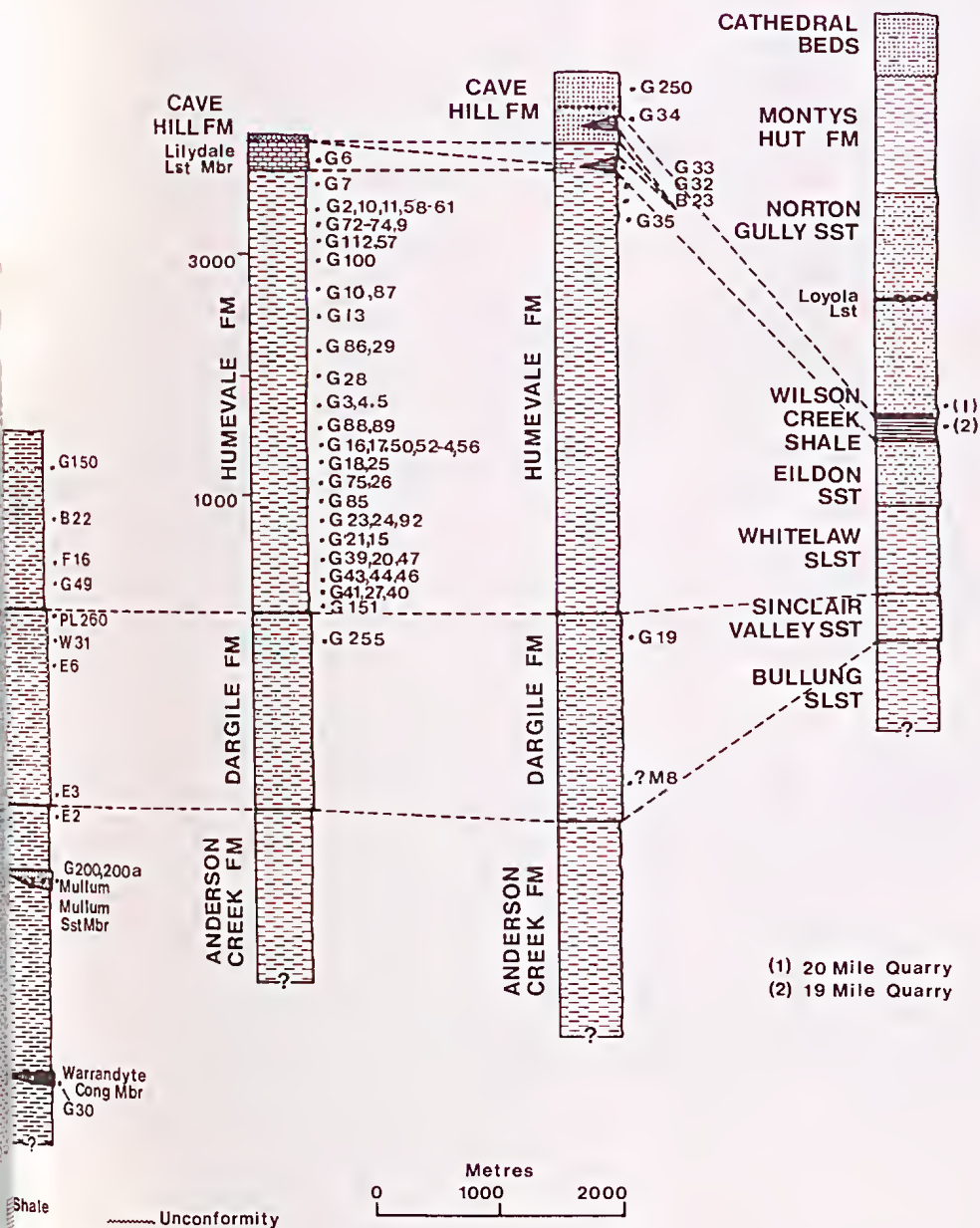


Fig. 3 – (continued)

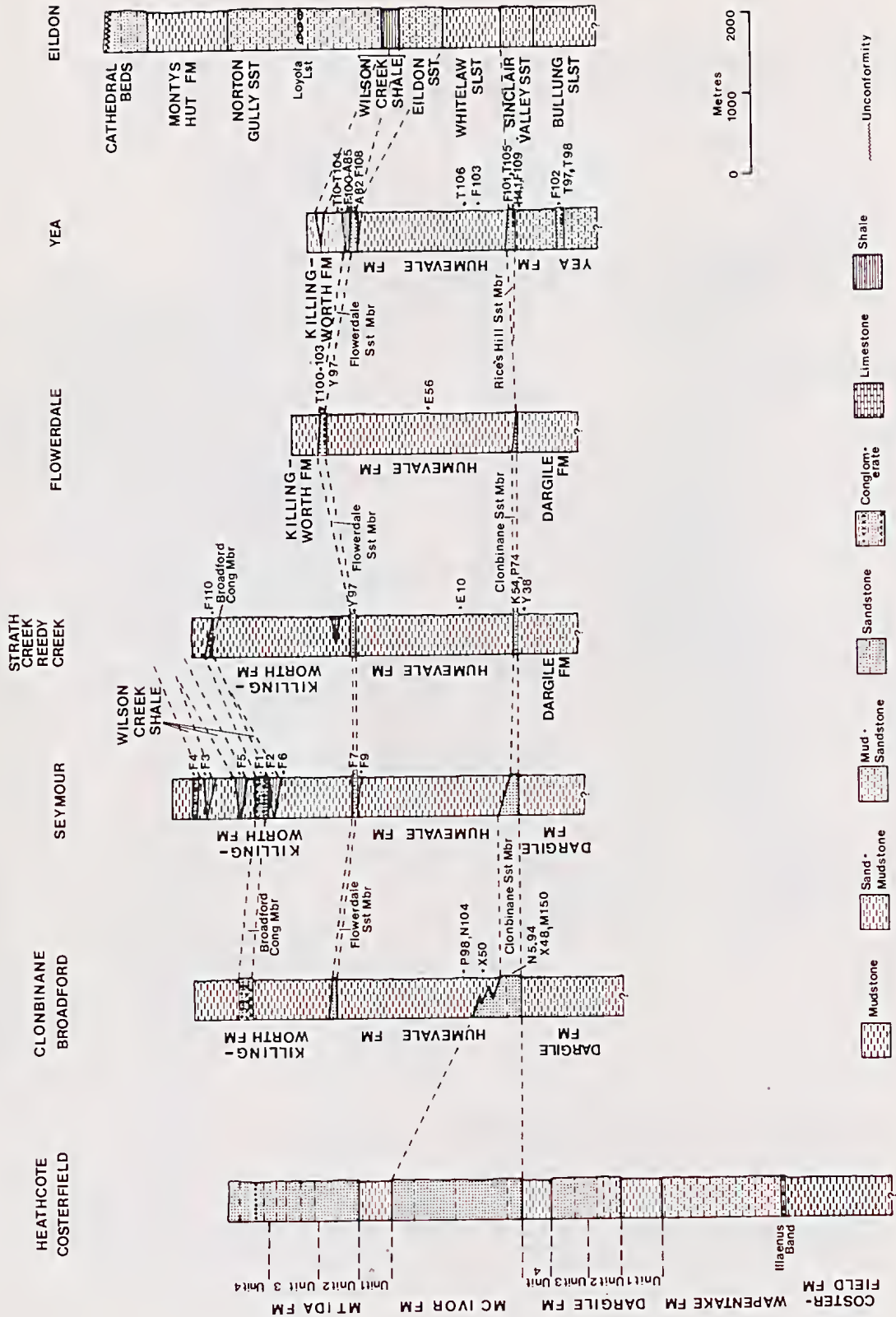


Fig. 4—Composite lithostratigraphic correlation of Silurian-Devonian of north central Victoria. Note that the fossil locality captions are published as for Clonbinane, Strath Creek, Flowerdale and Yea (Williams 1964) and Seymour (Schleiger 1964). Other localities not included in the above publications are listed by Garratt (1981, unpubl.).

Seymour, Eildon and Matlock these graptolite assemblages occur with elements of the *Baragwanathia* flora and the Tanjilian shelly assemblage—*Nowakia acuarina*, "*Panenka*" and "*Orthoceras*".

The presence of *M. aequabilis notoaequabilis* in the Wilson Creek Shale provides a link with the Bohemian sequence of central Europe where it is found in association with *M. yukonensis* in the Dvorce-Prokop Limestone which is considered by Jaeger (1970, 1979), and Strusz (1972, p. 445) to be 'late' Pragian in age, but nowhere in Australia is it found in association with *M. aequabilis notoaequabilis*.

In the northern Canadian Corillera, Lenz, (1979) has described a Pragian graptolite assemblage from the Road River Formation exposed in the Peel River. He recorded *M. fanicus* 215 m below beds containing *M. cf. thomasi* and 45 m above beds containing *M. aequabilis notoaequabilis*. He correlated this sequence with the *fanicus* zone at Tien Shan which Koren (1974, 1975) considered as Pragian. She noted the long vertical range of *M. aequabilis notoaequabilis*. Unfortunately *M. thomasi* has not been recorded from the Tien Shan. Jaeger (1979) placed the *thomasi* zone in the 'late' Pragian overlying the *fanicus* zone. This would be supported by Lenz's (1979) work in northern Canada, if his provisional identification of *M. thomasi* can be confirmed. The evidence provided by the conodont and brachiopod zonations of Nevada however, suggests that the *thomasi* zone is an 'early' rather than 'late' Pragian zone (Klapper 1977, Johnson 1977a, b). It must be emphasised that as yet no Pragian conodont zonation for the Bohemian succession has been established, although H. Jaeger (1980 pers. comm.), has noted that Schlonlaub has discovered *Icriodus pedavis pesavis* associated with *hercynicus* zone graptolites in the upper beds of the Lochkov Formation. For this reason the *pedavis pesavis* zone is here considered to be 'late' Lochkov (Fig. 2). Two critical sections, one in Nevada, and the other in Victoria indicate that the *thomasi* zone is partly coeval with the *Eognathodus sulcatus sulcatus* zone, here considered to be 'early' Pragian. *Monograptus thomasi* is found in the type section of the Rabbit Hill Limestone, Nevada (Berry & Murphy 1972, Matti *et al.* 1975), a short distance below an assemblage of brachiopods and conodonts (Johnson 1973, 1974) which Johnson (1977b) assigned to the *Spinoplasia* zone (Johnson 1965, 1970). This zone succeeds the 'late' Lochkov *Quadrithyrus* zone and belongs to the Pragian (Johnson 1977a, 1977b). Klapper (1977) assigned the conodonts from this part of the section to the *sulcatus sulcatus* zone. At both Jacobs Creek, near Tyers, and along the Thomson River in the eastern part of the Melbourne Trough, blue-black shales on strike with the Wilson Creek Shale to the north are interbedded with thin micritic limestones. At Jacob's Creek the shales contain *Monograptus thomasi*. The limestones contain the conodonts *Eognathodus sulcatus sulcatus* and *E. trilinearis* (Cary & Bolger in prep). Thus the *thomasi* zone correlates with the *sulcatus sulcatus* zone and evidence given here suggests that the Victorian sections

also correlate with the Rabbit Hill section of Nevada, U.S.A.

CONODONT ASSEMBLAGE ZONES

These are briefly discussed because their occurrence within the restricted limestones of the Early Devonian helps to place an upper age limit to 1, the upper beds of the Humcvale Formation at Lilydale and Seville, 2, the Boola Beds at Tyers, and 3, the widely distributed Wilson Creek shale.

Eognathodus sulcatus sulcatus ASSEMBLAGE ZONE

The *sulcatus sulcatus* assemblage zone (Fahreus 1971, Klapper 1977) as used in Australia by Klapper & Zeigler (1979) has been recognised in the Waratah, Coopers Creek and Lilydale Limestones of the Melbourne Trough (each represented by a single locality), principally through the works of Philip (1965), Philip & Pedder (1967), Strusz (1972), Argent (1971 unpubl.), and Cooper (1973b), in NSW (Druce 1970, Pickett 1980), in the Yukon territory (Fahreus 1971, Klapper 1977), and in Germany (Al-Rawi 1977). The type locality of *E. sulcatus sulcatus* is the old Tyers Limestone Quarry (loc. 11 of Philip 1962) on the east bank of the Lower Tyers River, Gippsland, Victoria (Philip 1965). All the Victorian occurrences of *E. sulcatus sulcatus* from the Lilydale, Waratah and Coopers Creek Limestones are considered coeval and 'early' Pragian in age.

CONODONT OCCURRENCES ABOVE THE *SULCATUS SULCATUS* ASSEMBLAGE ZONE

Eognathodus trilinearis and *Polygnathus* sp. are known from the Loyola Limestone of Loyola (Cooper 1973b). The Loyola Limestone is stratigraphically 1000 m above the Coopers Creek Limestone and Wilson Creek Shale (Figs 2, 3). This level may be as high as the *dehiscens* zone. Such an assignment would depend upon the identification of *Polygnathus* sp. However the inclusion of *E. trilinearis* in the Loyola Limestone, known to occur with *E. sulcatus sulcatus* at Jacob's Creek would suggest that the Loyola Limestone is no younger than *sulcatus* n. sub. sp. zone. The exact dating of the Loyola Limestone is further complicated because stratigraphic relationships between the limestone and the surrounding sediments is unclear. The Loyola Limestone is included within a thick matrix-supported conglomerate unit with both rounded clasts and angular contorted mudstone clasts and VandenBerg (1975b) has suggested that the limestone pods may be megaclasts.

Nowakia acuarina ASSEMBLAGE ZONE

The *Nowakia acuarina* assemblage zone (Boucek 1964) was recognised in Australia by Lütke (1979), and ranged from 'late' Lochkov to 'early' Pragian. *N. acuarina* is widely distributed in the Melbourne Trough (Talent 1965b, Talent & Banks 1967, VandenBerg 1975b, VandenBerg *et al.* 1976, Cooper 1973a). It occurs as a distinct 'marker' horizon in the Norton Gully Sandstone, throughout the eastern half of the Melbourne Trough. In the western portion of the Melbourne

Trough *Nowakia acuaria* is found in association with *M. thomasi* immediately above the Flowerdale Sandstone Member of the Killingworth Formation at Yea (loc. F100), Seymour and Strath Creek (Garratt 1979). At Lilydale, it occurs in the upper beds of the Humevale Formation (locs. G1, G2, G9 and G87) and at Seville in the Cave Hill (Figs 2, 3). The upper beds of the Humevale Formation are considered 'late' Lochkov in age because they conformably underlie the *sulcatus* sequence while *N. acuaria* makes its first appearance within the *Monograptus hercynicus* zone of the 'late' Lochkov (Lütke 1979). Other occurrences of dactyloconarid species are known at Lilydale at various horizons within the Humevale Formation (VandenBerg 1975b, VandenBerg *et al.* 1976), but they are yet to be studied in detail.

BRACHIOPOD ASSEMBLAGE ZONES

Although brachiopods are found sporadically in the Llandovery and Wenlock of the Melbourne Trough (see Fig. 2) it is not until the Ludlow that the faunas are sufficiently abundant to allow for the delineation of Assemblage Zones. During the Late Silurian the benthos is largely confined to the western margin of the trough from Heathcote, south, through Kilmore to Melbourne. However, by the Early Devonian, favourable environments extended into the Kinglake and Lilydale areas and locally near the eastern margin. Shelly faunas of the Llandovery and Wenlock strata have been described from Heathcote (Öpik 1953), Warrandyte (Gill 1952), and Springfield as reported by Talent *et al.* (1975).

The brachiopod assemblage zones of southeastern Australia (Fig. 2) are dated by either:

- (1) graptolites, conodonts and/or dactyloconarids occurring at the same locality or in the same stratigraphic section as the brachiopod assemblages.
- (2) correlation of the brachiopod assemblage zones with sections elsewhere in the Lachlan Fold Belt.
- (3) correlation of brachiopod assemblage zones with sections outside Australia (e.g., New Zealand, North America, Europe and Asia).
- (4) stratigraphic mapping of sediments in the Melbourne Trough.

The five brachiopod assemblage zones are regarded as being equivalent to the Yeringian of Gill (1965). Strusz's (1972) distinction of three faunas within this interval, (i.e., the Lower Yeringian Fauna, Upper Yeringian Fauna, and the Tabberabbera Fauna) is not accepted. 'Yeringian' faunal elements previously considered to be indicative of the uppermost Silurian and Lower Devonian (Talent 1965a, b, Strusz 1972), extend down into lower Ludlow (= Melbourneian of Gregory 1903). For example, *Pleurodictyum megastomum*, *Lissatrypa lenticulata*, *Notoconchidium thomasi*, *Maoristrophia banksi*, *Plectodonta bipartita* and *Leptostrophia plateia* are found in strata in varying associations with lower to upper Ludlow graptolite zones at Kilmore, Whittlesea and Melbourne.

In the correlation between different areas of the Melbourne Trough the influence of sediment type as a control of faunas cannot be underestimated. For example, there is a contrast between the faunas of the shallow neritic sandstones of the Heathcote and Clonbinane districts with those of the shallow neritic mudstones of the Lilydale district. The preservation of the assemblages in the McIvor and Mt Ida Formations may be poor compared with the mudstones of the Lilydale sequence. The differences are regarded as due to ecological control.

HEATHCOTE (sandy)	LILYDALE (muddy)
<i>Salopina</i> sp. nov. A	<i>Salopina</i> sp. nov. B
<i>Leptostrophia plateia</i>	<i>Leptostrophia alata</i>
<i>Maoristrophia banksi</i>	<i>Maoristrophia keblei</i>
<i>Mesodouvillina linbinura</i>	<i>Mesodouvillina lilydalensis</i>
<i>Notoleptaena otophera</i>	<i>Notoleptaena linguifera</i>
<i>Strophonella gippslandica</i>	<i>Hipparionyx major</i>
<i>Notoconchidium thomasi</i>	<i>Cymostrophia euglyphoides</i>
<i>Molongia</i> sp. nov.	<i>Gypidula victoriae</i>

However, some forms with wider ecological tolerance (for example, *Aegiria thomasi*, the Notanopliidae, Cyrtidina and the Spiriferidina) are found in sandy, muddy and limey facies between Heathcote, Kinglake, Lilydale and Tyers, and the ranges of the species in these groups are considered to be biostratigraphically important.

AEGIRIA THOMASI ASSEMBLAGE ZONE

The base of the *A. thomasi* zone is defined by the appearance of *A. thomasi* which has a wide geographic distribution and ranges throughout the zone. *Amphistrophia lyelli* and *Hedeina* sp. nov. are diagnostic of the *A. thomasi* zone, but have only been found at Kilmore (Fig. 6). *Lissatrypa lenticulata*, *Leptaena* sp., *Leptostrophia plateia*, *Isorthis* sp. nov. A, *Salopina* sp. nov. A, 'Protochonetes' *melbournensis*, *Nucloespira* sp. nov., *Molongia* sp. nov., *Camamotoechia* sp., and *Stegerhynchus* sp. appear at different intervals within the *A. thomasi* zone and with the exception of 'P' *melbournensis*, range into the succeeding zones (Figs 5, 6, 7).

The type locality for the zone is at Heathcote (Thomas 1937), where it includes Units 2, 3 and 4 of the Dargile Formation and it is also recognised between Kilmore, Whittlesea and Melbourne. In the upper part of the zone *A. thomasi* increases in abundance and together with the trilobite *Encrinurus simpliciculus* dominates the lower beds of Unit 4 of the Dargile Formation between Heathcote and Whittlesea.

The base of the *A. thomasi* zone lies within the *nilssoni* zone at Heathcote, Melbourne and Whittlesea (Fig. 2). *Saetograptus varians*, *S. chinaera*, *Lobograptus colonus* and *Bohemograptus bohemicus* are found in varying combinations at Heathcote, Whittlesea and Melbourne either at the same locality (e.g., F31, Kilmore East), or close by and along strike (compare Figs 2, 3 with Figs 5, 6 and 7), to localities yielding *A. thomasi*. The upper boundary of the *A. thomasi* zone cannot be satisfactorily linked with a graptolite zone. At

locality F10, Whittlesea, *B. bohemicus* occurs in the upper 50 m of the *A. thomasi* zone, indicating a Ludlow age for the top of the zone. At Heathcote, the top of the zone is marked by a facies change from mud to sand and for the next 1700 m of strata none of the enclosing fauna is diagnostic of either the Late Silurian or Early Devonian. The *A. thomasi* Zone may occur in the Bullung Siltstone of the Warburton-Matlock district, where VandenBerg (1975b, p. 8) recorded a suite of shelly fossils including *Aegiria* sp., *Lissatrypa* sp., *Plectodonta* sp., *Macropleura* sp., *Pleurodictyum megastomum* and *Encrinurus* sp.

NOTOPARMELLA PLENTIENSIS ASSEMBLAGE ZONE

The type locality of the *plentiensis* zone is at Upper Plenty, north of Whittlesea, in the lower beds of the Humevale Formation.

The base of the zone is defined by the sudden appearance of many new forms including *Notoparmella plentiensis*, *Plectodonta bipartita*, *Salopina* sp. nov. B, '*chonetes*' sp. nov. B and *Maoristrophia banksi* in the lowest beds of the Humevale Formation. Rare specimens of *N. plentiensis* are found in Unit 4 of the Dargile Formation but it increases in abundance in the lower 600 m of the Humevale Formation at Upper Plenty where it dominates the fauna together with occasional specimens of *Lissatrypa lenticulata* (long ranging) *Gracianella* sp. nov., *Isortilis* sp. nov., *Salopina* sp. nov. B, and '*Eatonia*'-like rhynchonellids.

Between Christmas Hills and Lilydale, the *plentiensis* Zone is recognised by an impoverished fauna of *Notoparmella plentiensis*, *Plectodonta bipartita*, *Gracianella* sp. nov., *Howellella nucula* subsp. nov., rare *Maoristrophia banksi*, *Notanoplia panifica* and *Salopina* sp. nov. B. The Zone extends from the upper beds of the Dargile Formation to the lower 400 m of the Humevale Formation (Fig. 5). This assemblage contrasts with the richly diverse assemblage at Kinglake, suggesting an increasing water depth east from Kinglake at this time (Williams 1964, Garratt in press).

At Heathcote, *Notoparmella plentiensis*, *Gracianella* sp. nov. and *Notanoplia panifica* are absent. But the *plentiensis* zone is recognised by the appearance of *Maoristrophia banksi*, *Notoconchidium thomasi* and *Salopina* sp. nov. B., all of which appear in the *plentiensis* zone at Kinglake. Locally at Heathcote, *Sowerbyella plebeia* appears in this faunal interval. In the Flowerdale-Yea district the *plentiensis* zone is represented by the rare and probably allochthonous occurrence of *Notoparmella plentiensis*, *Maoristrophia banksi*, *Howellella* cf. *nucula* subsp. nov. and rhynchonellids at localities H1 and H4. *H. cf. nucula* subsp. nov. also occurs at F101 and F102 at Yea. These localities are scattered through 100 km, of the Yea Formation through to the overlying Rice's Hill Sandstone Member (Fig. 4).

The Ludlow age for the *plentiensis* zone is based on six widely scattered graptolite localities occurring either below or within the *plentiensis* zone:

1, loc. F10, Upper Plenty: *Bohemograptus bohemicus*

occurs 100 m below the base of the *plentiensis* zone in Unit 4, Dargile Formation (Williams 1964).

2, loc. X50, Reedy Creek: *Pristiograptus* cf. *haupti* occurs 100 m above the base of the *plentiensis* zone in Humevale Formation.

3, loc. E10, between Strath Creek and Reedy Creek: *Bohemograptus bohemicus*, *Pristiograptus* sp. and *Linograptus* sp. are found approximately 900 m above the base of the *plentiensis* zone (Garratt 1979) in Humevale Formation.

4, loc. E56, Flowerdale, *Monograptus* cf. *uncinatus* occurs approximately 900 m above the base of the *plentiensis* zone in Humevale Formation (Williams 1964).

5, loc. H1, Yea, *M. cf. uncinatus uncinatus* occurs immediately below the Rice's Hill Sandstone Member (and approximately 100 m above the base of the *plentiensis* zone) (R. B. Rickards 1980 written communication).

6, loc. H4, Yea: *B. bohemicus* occurs at the same stratigraphic level as (5), (G. Packham 1977 written communication, R. B. Rickards 1980 written communication).

Thus the basal half of the *plentiensis* zone at Clonbinane, Yea and Kinglake can be no older than early Ludlow. The upper boundary of the zone cannot be related to either graptolite or conodont zones owing to the complete absence of established Pridolian to Lochkovian graptolites and conodonts in the Melbourne Trough.

BOUCOTIA JANAEE ASSEMBLAGE ZONE

The base of the *janaea* zone is defined by the abrupt appearance of abundant *B. janaea*, and nine other species, many of which are important in delineating the Silurian-Devonian boundary at Lilydale (Fig. 5). Fifteen other brachiopod species appear about 200 m higher in the section. This zone comprises Strusz' (1972) "Lower Yeringian Fauna". Seven of the species occurring in the *janaea* zone at Lilydale appear at the same stratigraphic level in the Kinglake district. There are: *B. janaea*, *Salopina* sp. nov. A, '*Protochonetes*' *ruddockensis*, *Leptostrophia alata*, *Cymostrophia euglyphoides*, *Notoleptaena otophera*. All but *Salopina* sp. nov. A. are important in delineating the Silurian-Devonian boundary in the Kinglake district. At Heathcote the base of the *janaea* zone is recognised by the appearance of *B. janaea* (occasional), '*Protochonetes*' *ruddockensis*, *Plectodonta bipartita*, *Mesodouvillea limbimura*, *Notoleptaena linguifera*, *Meristella* sp. nov. and *Cyrtina* sp. nov. Of these, the latter is important in the delineation of the Silurian-Devonian boundary at Heathcote. This boundary is about 100 m above the base of Unit 1 of the Mount Ida Formation (Fig. 7).

BOUCOTIA AUSTRALIS ASSEMBLAGE ZONE

The *australis* zone is found at many localities in Victoria, New South Wales and Tasmania. In Victoria, the *australis* zone is well developed at Lilydale, Kinglake, Heathcote and Tyers, near the eastern margin of the Melbourne Trough. The base of the *australis* zone is recognised by the appearance of *Boucotia australis* and fifteen other brachiopod species at about 1500 m above

the base of the Humevale Formation. Of these *Schizophoria* sp. nov. A., '*Protochonetes*' *cresswelli*, '*P*' *robusta*, *Cynostrophia* *cresswelli*, *Strophonella* sp. nov., *Hipparionyx* *major*, *Gypidula* sp. nov., *Coelospira* *australis*, *Meristella* *australis* and *Hysterolites* *lilydalensis* are locally abundant. At Kinglake the base of the *australis* zone is about 1600 m above the base of the Humevale Formation, and locally abundant forms such as *Boucotia* *australis*, *Notanoplia* *philipi*, *N. pherista* indicate a correlation of this level with that at Lilydale. Very rare occurrence of *Cyrtinopsis* *cooperi*, *Hysterolites* *lilydalensis*, *Muriferella* sp., *Boucotia* *withersi*, *Strophonella* *gippslandica*, *Australocoelia* sp. nov. and *Eospirifer* *eastoni* support this correlation.

The base of the *australis* zone at Heathcote is defined by the appearance of *Boucotia* *australis*, *Cyrtinopsis* *cooperi*, *Hysterolites* *lilydalensis*, *Strophonella* *gippslandica* and *Australocoelia* sp. nov. in Unit 3 of the Mount Ida Formation in the Parish of Redcastle. The *australis* zone is clearly recognisable in the upper sandstones and muddy sandstones of the Boola Formation at Tyers (Philip 1962). Where the assemblage includes *Boucotia* *australis*, *Notanoplia* *philipi*, *Schizophoria* sp. aff. *S.* sp. nov. A, *Maoristrophia* *keblei*, *Strophonella* *gippslandica*, *Notoleptaena* *otophera*, *Leptostrophia* *affinilata*, *Cynostrophia* *euglyphoides*, '*Protochonetes*' *cresswelli*, *Spirigerina* *supramarginalis*, *Hewellessa* *scabra*, and rare *Hysterolites* *lilydalensis*. The latter species has been found by me in muddy sandstone immediately below the Coopers Creek Limestone at Tyers. *L. affinilata* is not known elsewhere in the Melbourne Trough from the *australis* zone.

BOUCOTIA LOYOLENSIS ASSEMBLAGE ZONE

The base of the *loyolensis* zone at Lilydale is defined by the appearance of six new species (Fig. 5) including abundant *Leptostrophia* *affinilata*, '*Parachonetes*' *baragwanathi*, *Mesodouvillina* *lilydalensis* and *Ambocoelia* sp. nov. *B. loyolensis* first appears as a rare species in the upper part of the *australis* zone. At a higher level in the *loyolensis* zone a very large *Schizophoria* species appears, together with *Nadiastrophia* sp., *Australocoelia* sp. nov., *Acrospirifer* sp. nov. A., *Eurekaspirifer* sp., *Cyrtina* cf. *heteroclita* *gregale* and *Uncinulus* sp. nov. B. These species are important in correlation with Tabberabbera, North America and China. The base of the *loyolensis* zone lies approximately 2 500 m above the base of the Humevale Formation and extends up into the overlying sandstones of the Cave Hill Formation at Seville, east of Lilydale (Fig. 5).

At Yea and Flowerdale the *loyolensis* zone is represented by an allochthonous assemblage found in the graded sandstones, matrix-supported and clast-supported conglomerates of the Flowerdale Sandstone Member and the Broadford Conglomerate Member at Strath Creek. These transported assemblages include those which are typical of the *australis* zone, in particular the brachiopod species occurring in the Flower-

dale Sandstone Member (localities T100-T104, Y97) at Flowerdale, for example, *Boucotia* *australis*, *Plectodonta* *bipartita*, *Isorthis* *festiva*, *Tyersella* *typica*, *Leptostrophia* *alata*, *Cynostrophia* *cresswelli*, *Eospirifer* *eastoni* and *Hewellessa* sp., whilst further east (localities F110, F104, A85) at Yea and Strath Creek the same stratigraphic horizon yields *Boucotia* *australis*, *B. loyolensis*, *B. withersi*, *Tyersella* *typica*, *Isorthis* *festiva*, *Leptostrophia* *alata*, *L. affinilata*, *Hysterolites* *lilydalensis*, and *Eospirifer* *eastoni* which are typical of the *loyolensis* zone at Lilydale.

In the vicinity of Eildon and Jamieson, the *loyolensis* zone occurs at isolated localities within the lower 1 000 m of the Norton Gully Sandstone (Bell 1961) where it is represented by a low diversity allochthonous fauna. The fauna includes *Boucotia* *loyolensis*, *B. australis*, *Leptostrophia* *affinilata*, *Hysterolites* *lilydalensis*, *Hipparionyx* *major*, *Notoleptaena* *undulifera* and *Acrospirifer* sp. nov. At Griffiths Quarry, Loyola, near Mansfield, twenty-three brachiopod species, many represented by single specimens, have been recognised from collections stored in the National Museum of Victoria. The species are found in pebbly mudstones and include: *Boucotia* *loyolensis*, *B. australis*, *Leptostrophia* *affinilata*, *L. alata*, *Cynostrophia* *euglyphoides*, *Nadiastrophia* cf. *superba*, *Mesodouvillina* *lilydalensis*, *Hipparionyx* *major*, *Notoleptaena* *otophera*, *N. undulifera*, *Leptaena* sp. nov., '*Parachonetes*' *baragwanathi*, *Maoristrophia* sp. nov., *M. keblei*, *Reeftonia* *alpha*, *Gypidula* sp. nov., *Eospirifer* *eastoni*, *Hewellessa* sp., *Hysterolites* *lilydalensis*, *Acrospirifer* sp. nov. and *Cyrtina* cf. *heteroclita* *gregale*. This greatly expands the previous known assemblage from Loyola, and all species listed are important in the correlation between Lilydale and Tabberabbera, Victoria, NSW and New Zealand.

The base of the *loyolensis* zone at Lilydale is about 1 700 m below the base of the Lilydale Limestone Member, which it has been argued elsewhere in this paper is 'early' Pragian in age. The plant-graptolite beds (the upper plant graptolite Horizon of Couper (1965)), which is interbedded with the *loyolensis* zone at Seymour, Yea and Flowerdale is also regarded as early Pragian (Garratt 1979). Likewise at Eildon, where the *loyolensis* zone overlies the Wilson Creek Shale (equivalent to the upper plant-graptolite Horizon of Yea) an 'early' Pragian age is suggested. The top of the *loyolensis* zone which probably coincides with the Loyola Limestone at Loyola contains *Eognathodus* *trilinearis* and *Polygnathus* sp. (Cooper 1973b), suggesting a late Pragian age. Thus on present evidence the *loyolensis* zone ranges from 'early' to 'late' Pragian.

OCCURRENCES OF BRACHIOPOD ASSEMBLAGE ZONES OUTSIDE THE MELBOURNE TROUGH

The *Aegiria* *thomasi* zone has not been recognised elsewhere in the Lachlan Fold Belt and this may reflect the scarcity of published work on Silurian brachiopod faunas in Australia.

The *plentiensis* zone may be present in the Yass Basin, New South Wales (Brown 1941), and the Dundas Trough, Tasmania. The Yarwood Siltstone Member of the Black Bog Shale (Link 1970) at Yass has yielded, amongst other species, *Hedeina bowringensis* and *Plectodonta bipartita* (identified from Australian Museum collections). This horizon is overlain by shales containing *Bohemograptus bohemicus* and *Linograptus posthumus posthumus* and was assigned to the late Ludlow by Link (1970). This suggests that the Yarwood Siltstone Member is 'mid' Ludlow in age and broadly correlates with the *plentiensis* zone of the Melbourne Trough. Further, the conodont fauna of the Yarwood Siltstone Member was correlated with that of the *latiolatus* zone by Link and Druce (1972).

The Florence Sandstone (Talent & Banks 1967) outcrops near Zeehan and Queenstown in the Dundas Trough, Tasmania. It has yielded a very similar fauna to that occurring in the *plentiensis* zone at Whittlesea and Upper Plenty. It includes *Hedeina denslineata*, Ambocoelidae gen. et sp. nov., *Isorthis* sp. nov., *Salopina* sp. nov., *Maoristrophia banksi* and *Leptostrophia plateia*. This list is based on collections from the National Museum of Victoria. The only other noteworthy species so far described from the Florence Sandstone are *Notoconchidium florencensis*, *Strophonella australiensis* and *Amphistrophia lyelli* (Gill 1950). *Maoristrophia* has been recorded from the underlying Austral Creek Siltstone at Princess River, Tasmania together with the late Wenlock graptolite *Monograptus vulgaris* (Talent & Banks 1967, p. 158). Even allowing for the apparent absence of *Notoparmella plentiensis* and *Notanoplia parifica* from the Tasmanian sequence, the *plentiensis* Assemblage Zone appears to represent most of the thickness of the Florence Sandstone, giving an approximate late early Ludlow age for the basal beds of the Florence Sandstone thereby confirming Philip's (1967, p. 918) correlation for this part of the Tasmanian sequence. The Skalian (= Pridolian) age given by Talent & Banks (1967, p. 152) for the same section is not accepted.

The recognition of the *janaea* zone outside the Melbourne Trough is yet to be determined but two possible areas occur in New South Wales - Manildra (Savage, 1968) and Bungonia (Jones *et al.* 1981). Near Manildra, New South Wales, Savage (1968) recorded an assemblage from near the top of the Fairhill Formation including *Dolerorthis* cf. *persculpta*, *Isorthis* cf. *festiva*, *Howellella* cf. *scabra*, *Eospirifer parahentius* (synonym of *E. eastoni*), *Schizophoria* sp., *Spirigerina* cf. *supramarginalis* and *Plectodonta bipartita*. Savage was unable to assign this assemblage to a precise horizon of the Lower Devonian, and the overlying Maradana Shale contains an assemblage which clearly belongs to the *australis* zone. The assemblage from the Fairhill Formation indicates an age ranging from *janaea* to *australis* zone. Certainly *Eospirifer eastoni* and *Schizophoria* sp. strongly support a Devonian age for the assemblage. Strusz (1972, p. 442) drew attention to the absence of *Notoconchidium* in the Fairhill Formation, and con-

cluded that the top of the formation was significantly above the base of the Devonian. However the distribution of *Notoconchidium* in the Melbourne Trough is strongly influenced by environment and its absence here may be related to water depth and/or lithofacies rather than age.

The *australis* zone is widely recognised in New South Wales and Tasmania. The fauna recorded and described from the Bell Shale (above the so-called "transition beds") of Tasmania by Gill (1948, 1950), and Talent & Banks (1967), includes *Notanoplia pherista*, *Australocoelia polyspera*, *Mesodouvillina lilydalensis*, *Maoristrophia keblei* and *Notoleptaena otophera*. *Boucotia australis* is apparently absent from the Bell Shale Assemblage. In New South Wales the *australis* zone is found in the Mullamuddy Formation at Mudgee, the Waterbeach Formation at Limekilns and the Maradana Shale at Manildra. From the Mullamuddy Formation, Wright (1967b), Wright in Strusz (1972) and Wright (1978, oral communication) recorded a suite of brachiopods including *Dolerorthis* cf. *persculpta*, *Strophonella* sp., *Gypidula* sp., *Spirigerina supramarginalis*, *Crytina* sp., *Hysterolites* and *Cyrtinopsis cooperi*, and is indicative of the *australis* zone. The Waterbeach Formation has yielded forms such as *Dolerorthis* sp., *Schizophoria* sp., *Boucotia australis*, *Eospirifer eastoni* and *Spirigerina supramarginalis* (Wright, 1967b). From the Maradana Shale of Manildra, New South Wales, Savage (1974) described *Skenidioides* sp., *Dolerorthis* sp., *Resserella elegantuloides*, *Dalejina* aff. *frequens*, *Muriferella* sp., *Mesodouvillina* cf. *limbinnura*, *Leptostrophia affinitata*, *Notanoplia pherista*, *Gypidula* cf. *victoriae*, *Cyrtinopsis cooperi*, *Quadrithyrus* cf. *robusta*, *Cyrtina* sp., *Spirigerina supramarginalis* and *Leptocoelia*, indicative of at least the *australis* zone. None of these four species occur beneath the *australis* zone in Victoria. The other species described by Savage are either long-ranging or not recorded from Victoria. Strusz (1972) recorded a brachiopod fauna from low in the Garra formation at Wellington including *Boucotia australis*, *Cymostrophia stephani*, *Isorthis festiva*, *Notoleptaena* cf. *otophera*, *Muriferella* cf. *punctata* and an *australis* zone is suggested. The *loyolensis* zone marks the top of the Yeringian fauna at Lilydale, Loyola and Tabberabbera, where it is found in the Dead Bull and Kilgower Members of the Tabberabbera Formation at Tabberabbera. The faunal information is provided by Talent (1963) and Talent (1972).

LILYDALE	LOYOLA	TABBERABBERA
<i>Boucotia loyolensis</i>	<i>B. loyolensis</i>	
<i>B. australis</i>	<i>B. australis</i>	
<i>Plectodonta bipartita</i>		<i>P. bipartita</i>
<i>Isorthis allani</i>	<i>Reeftonia alpha</i>	<i>R. alpha</i>
<i>Schizophoria</i> sp. nov. A		<i>Schizophoria</i> sp.

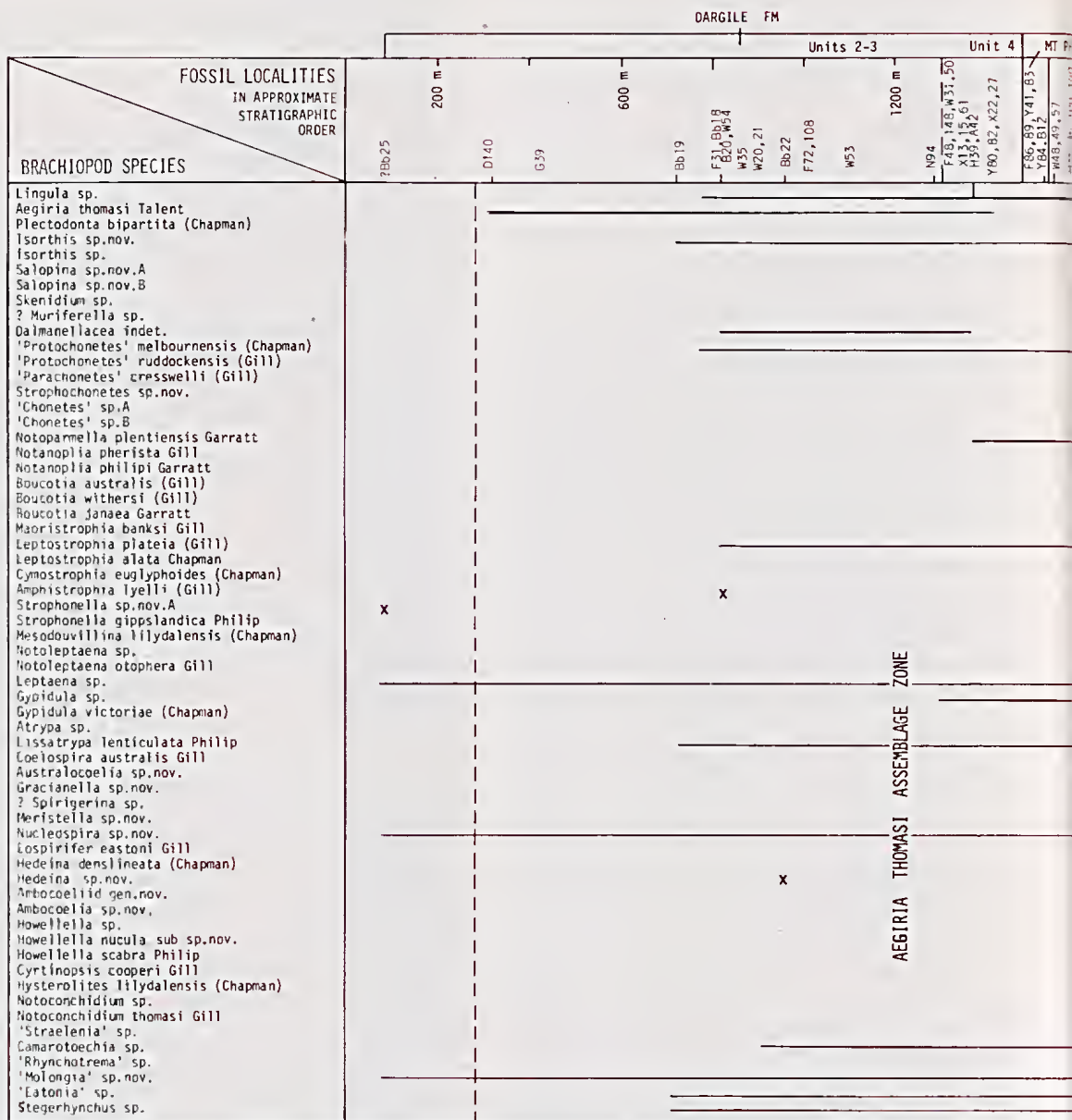


Fig. 6—Range chart of brachiopod species of the Kinglake-Whittlesea district, Victoria. The continuous horizontal lines intersect the known vertical range of the species in the area. The localities may or may not contain all the species indicated. The data on the distribution of brachiopods and assemblages at each locality is available from the author. The collections are stored in the National Museum of Victoria and the lists are prepared from collections made by A. Selwyn, N. Taylor, J. Jutson, R. Withers, G. Williams, E. Gill, T. Daragh and the author.

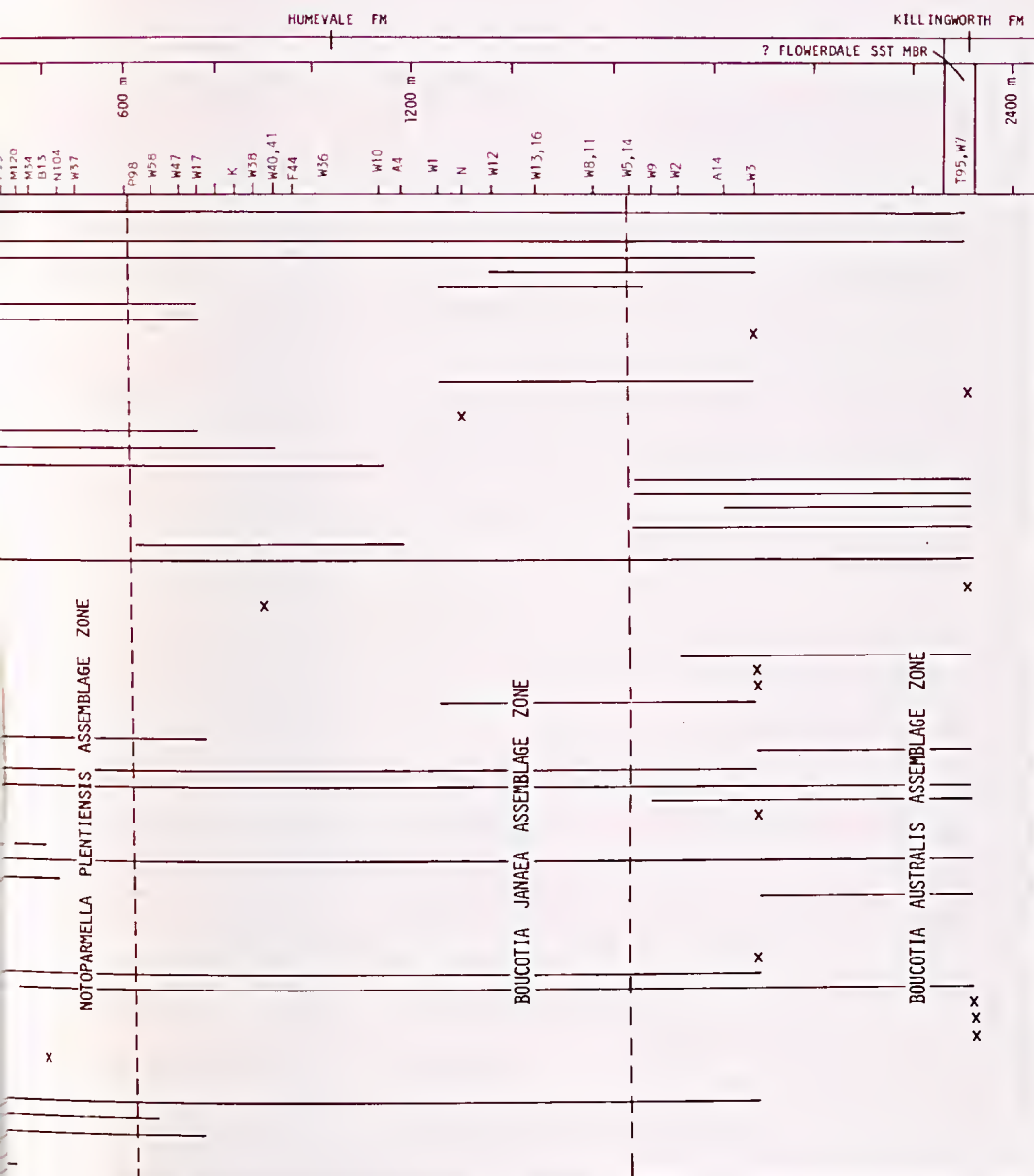


Fig. 6—(continued)

<i>Muriferella</i> sp.		<i>Muriferella punctata</i>
'Protochonetes' <i>baragwanathi</i>	'P.' <i>baragwanathi</i>	'P.' <i>baragwanathi</i>
<i>Leptostrophia alata</i>	<i>L. alata</i>	
<i>L. affinilata</i>	<i>L. affinilata</i>	<i>L. affinilata</i>
<i>Maoristrophia keblei</i>	<i>M. keblei</i>	
<i>Cymostrophia euglyphoides</i>	<i>C. euglyphoides</i>	<i>C. euglyphoides</i>
<i>Nadiastrophia</i> sp.	<i>N. cf. superba</i>	<i>N. superba</i>
<i>Notoleptaena otophera</i>	<i>N. otophera</i>	
	<i>N. undulifera</i>	<i>N. undulifera</i>
<i>Hipparionyx major</i>	<i>H. major</i>	<i>H. major</i>
<i>Mesodonvillina lilydalensis</i>	<i>M. lilydalensis</i>	
<i>Gypidula</i> sp. nov.	<i>G. sp. nov.</i>	<i>G. vultura</i>
<i>Lissatrypa lenticulata</i>		<i>L. lenticulata</i>
' <i>Spinatrypa</i> ' <i>fimbriata</i>	'S.' <i>fimbriata</i>	'S.' <i>perflabellata</i>
<i>Eospirifer eastoni</i>	<i>E. eastoni</i>	<i>E. eastoni</i>
<i>Howellella</i> sp. nov.	<i>Howellella</i> sp.	<i>H. textilis</i>
<i>Spiriferide</i> gen. nov.	<i>Spiriferide</i> gen. nov.	
<i>Acrospirifer</i> sp. nov.	<i>Acrospirifer</i> sp. nov.	
<i>Cyrtinopsis cooperi</i>		<i>C. cooperi</i>
<i>Hysterolites lilydalensis</i>	<i>H. lilydalensis</i>	<i>H. lilydalensis</i>
<i>Cyrtina</i> cf. <i>heteroclita gregale</i>	<i>C. cf. heteroclita gregale</i>	<i>C. heteroclita gregale</i>
<i>Uncinulus</i> sp. nov. A.		<i>U. calathuscus</i>
<i>Nucleospira</i> sp. nov.		<i>N. bellornata</i>
? <i>Eurekaspirifer</i> sp.		<i>Adolfia glypta</i>

It is apparent from the above lists that the fauna of the Dead Bull and Kilgower Members at Tabberabbera contain many elements common to Lilydale and Loyola. The differences may be due to facies or to age. Figure 3 shows that most of the faunas of the Dead Bull and Kilgower Members are younger than those from Loyola. An even more marked faunal change occurs between the Kilgower and Roaring Mag Members where new elements such as *Buchanathyris westoni*, *B. pulchra*, *B. ?* sp. A., *Hysterolites tritus*, *H. sp. C.* and *H. sp. E.* occur in the Roaring Mag Member; such an assemblage has affinities with the Buchan Caves Limestone and Bell Point Limestone assemblages which are dominated by *Spinella*, *Buchanathyris*, *Atrypa*, *Nadiastrophia*, *Cymostrophia*, corals and gastropods (Talent 1965b,

Talent & Banks 1967, Strusz 1972), and probably warrant delineation of one, or two assemblage zones. Sherwin's (1980) *Spinella* 'Zone' described from Cobar warrants future attention. However, more work is necessary on the biostratigraphy of these 'late' Pragian-Zlichovian brachiopod faunas of southeast Australia. At present the *loyolensis* zone is considered to extend up into the Kilgower Member of the Tabberabbera Formation. In the Queen's Pinch region of New South Wales, Wright (1966) reported the occurrence of *Nadiastrophia* cf. *superba*, *Muriferella punctata* and *Leptostrophia affinilata* from the middle of the Mulla muddy Formation; *Nadiastrophia* cf. *superba* and *Leptostrophia affinilata* from the Taylors Hill Formation; and *Dolerorthis* cf. *persculpta*, *Cyrtinopsis cooperi*, *Muriferella punctata* and *Nadiastrophia* cf. *superba* from the Ingleburn Formation. *Leptostrophia affinilata*, *Cyrtinopsis cooperi*, *Ivanothyris*, *Adolfia* and *Dolerorthis* cf. *persculpta* are also known from the Sutchers Creek Formation. All these assemblages suggest correlation with the *loyolensis* zone ("Tabberabberan Fauna"), the contacts between the various formations are fault bounded (Strusz, 1972, correlation chart), and may be coeval, depending upon the range of *Nadiastrophia* cf. *superba* and *Muriferella punctata*.

CORRELATION OF BRACHIOPOD ASSEMBLAGE ZONES OUTSIDE OF AUSTRALIA

Of the assemblage zones described herein, only the Devonian zones (*janaea*, *australis* and *loyolensis* zones) are important in correlation outside Australia. The *janaea* zone is discussed under the Siluro-Devonian Boundary. The base of the *australis* zone is considered to be of 'late' rather than 'early' Lochkovian age. The following forms appearing at or close to the base of the *australis* zone have value for correlation (those marked with an asterisk are of local value only), *Boucotia australis**, *Notanoplia philipi**, *Hysterolites lilydalensis*, *Cyrtinopsis cooperi**, *Muriferella* sp., *Cymostrophia creswelli**, and *Uncinulus* sp. nov. A*. Solle (1963) concluded from a study of *Hysterolites* that the top of the Ober Graptolithenschiefer in Thuringia is within the middle to middle upper Siegenian. Strusz (1972, p. 428) noted that the *hercynicus* zone ("Upper" Lochkovian) extends to the top of the Ober Graptolithenschiefer. It implies that *Hysterolites* arose in central Europe in the "late" Lochkov. Erben & Zagora (1967, p. 61) also noted that *Hysterolites* appeared in the "late" Lochkov in the Hercynian facies in Germany, and ranges through to the upper Emsian (Jahnke 1971). The appearance of *Hysterolites* at Lilydale, Heathcote and Kinglake is considered to indicate a "late" Lochkov age. At Lilydale, the base of the succeeding *loyolensis* zone contains Pragian brachiopod assemblages in an interrelationship with the *thomasi*, *acuaria* zone and *sulcatus sulcatus* zones ranging up to at least the *sulcatus* n. sub. sp. zone of the 'late' Pragian.

The appearance of local elements such as *Cyrtinopsis cooperi*, *Boucotia australis*, *Notanoplia philipi* and *Uncinulus* sp. nov. A are considered indicative of the 'late'

Lochkov in southeastern Australia. The rare occurrence of *Muriferella* in the *australis* zone at Lilydale, Kinglake and Manildra also suggest a 'late' Lochkov age; it is indicative of the 'upper' Lochkov *Spirigerina supra-marginalis* Unit at Royal Creek, Yukon (Lenz, 1977a, b).

From New Zealand the Baton River fauna (Shirley 1938, Wright 1967a), and the Reefton Fauna (Allan 1935, 1947, Boucot *et al.* 1963, Boucot *et al.* 1966, Gill *et al.* 1966), include elements which are common to the *loyolensis* zone of the Victorian sequence. However, both the Baton River and Reefton lists must be considered provisional, only those forms previously published are given. The faunas are in need of revision and include forms yet to be described.

LILYDALE	BATON RIVER	REEFTON
<i>Isorthis allani</i>	<i>I. allani</i>	<i>Reeftonia marwicki</i>
<i>Fascicostella</i> sp. nov.	<i>F. gervillei</i>	
<i>Schizophoria</i> sp. nov. A.	<i>S. provulvaria</i>	
<i>Leptostrophia</i> <i>affinilata</i>	<i>L. explanata</i>	<i>L. reeftonensis</i>
<i>M. lilydalensis</i>	<i>Mesodouvillina</i> sp.	
<i>C. euglyphoides</i>	<i>Cymostrophia stephani</i>	
<i>H. major</i>	<i>Hipparionyx minor</i>	
<i>E. eastoni</i>	<i>Eospirifer eastoni</i>	" <i>Hedeina</i> " <i>bensoni</i>
<i>Cyrtinopsis cooperi</i>	<i>C. cooperi</i>	
<i>Acrospirifer</i> sp. nov.	<i>A. 'arduennensis'</i>	<i>A. coxi</i>
<i>C. cf. heteroclita</i>	<i>Cyrtina heteroclita</i>	
<i>Spiriferide</i> gen. nov.		<i>Spiriferide</i> gen. nov.
<i>Hysterolites lilydalensis</i>	<i>H. cf. subspeciosus</i>	
<i>Maoristrophia keblei</i>		<i>M. neozelanica</i>

As can be seen from the faunal lists there are more species in common between Lilydale and Baton River than between Lilydale and Reefton, although *Reeftonia alpha* occurs at Loyola and Tabberabbera. The Baton River fauna has been assigned to the Siegenian (Shirley 1938, Boucot *et al.* 1969, p. 13) by correlation of the Baton River Beds with the Devonian of Europe (Shirley, 1938) and with Siegenian to early Emsian horizons at Lilydale and Tabberabbera (Boucot *et al.* 1969, p. 13). According to Boucot *et al.* the Reefton Beds are younger (early Emsian), thereby explaining the faunal differences between Baton River (Tasman Subprovince) and Reefton (New Zealand Subprovince). Equally, in view of the differences in sediment types between Reefton and Baton River (Wright 1967a), environmental factors such

as water depth, current activity and bottom sediment type, may have influenced the composition of the benthos. As yet no reliable published data on the age or faunal community relationships of the New Zealand Devonian sequences are known. They seem to correlate with the *loyolensis* zone; they are certainly older than the Buchanian fauna ('late' Pragian).

DISCUSSION OF THE SILURIAN-DEVONIAN BOUNDARY IN THE MELBOURNE TROUGH

The base of the *janaea* zone is believed to coincide approximately with the Silurian-Devonian boundary in the Melbourne Trough. Because of the absence of Pridoli and Lochkov graptolites and conodonts in the Melbourne Trough, discrimination of the Silurian-Devonian boundary, now accepted as being the base of the *uniformis* zone (McLaren 1977), must rest with the shelly fauna. The taxa which appear to be useful in delineating the base of the Devonian in Victoria include *Eospirifer eastoni*, *Cyrtina* sp. nov., *Boucotia janaea*, *Cymostrophia euglyphoides*, *Maoristrophia keblei*, *Leptostrophia alata*, *Schizophoria* sp. nov. A, and *Gypidula victoriae* of the *janaea* zone. In terms of world-wide distribution, *Cyrtina*, *Boucotia*, *Schizophoria* and *Cymostrophia* are essentially Devonian genera (but see Boucot 1977). Berdan *et al.* (1969) and Johnson (1966) note that *Cyrtina* is unknown from pre-Devonian strata. The record of a single specimen of *Cyrtina* from 25 m below the base of the *uniformis* zone in the Roberts Mountain Formation of the Birch Creek Section, Nevada, by Johnson, *et al.* (1973) has yet to be authenticated. Boucot's (1977) listing of *Cyrtina* from the Pridolian of the Cordilleran Province is probably based on this Nevada occurrence. No authenticated pre-Devonian occurrence of *Cymostrophia* is known. *Schizophoria* has been recorded from the Pridoli of the Cordilleran Province (Boucot 1977, p. 312, Lenz 1977a, p. 48) and as a rare genus in the Bohemian Province of central Asia (Nikiforova 1937, p. 7). In all other faunal provinces it appears at the base of the Devonian. *Boucotia* is not known in the Tasman subprovince from any zone earlier than the *janaea* zone.

Eospirifer eastoni, *Leptostrophia alata* and *Maoristrophia keblei* all appear at or close to the base of the *janaea* zone in the Melbourne Trough. The record of *Eospirifer* from the Pridolian of the Tasman subprovince by Boucot (1977, p. 314) rests on the yet to be confirmed age of the Mallee Tank Beds of the Cobar Region, New South Wales (Iten & Carter 1951), it is not known whether this species is *E. eastoni* or not.

ACKNOWLEDGEMENTS

My sincere thanks go to A. J. Wright for his advice, criticisms and suggested improvements to the manuscript. I also thank A. J. Boucot, G. M. Philip and O. P. Singleton who discussed aspects of the study with me; two anonymous reviewers for constructive suggestions and criticisms; and Jacky Daley and Carol Healy who drafted the figures. This work is published with the

permission of the Director of the Geological Survey of Victoria.

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APPENDIX

The following fossil names that appear in figures 5, 6 and 7 and throughout the text as unnamed new species are here listed with a National Museum of Victoria number prefixed with P. They are presently stored at the Geological Survey of Victoria on loan from the National Museum of Victoria.

FIGURE 5

<i>Salopina</i> sp. nov. B	P716
<i>Schizophoria</i> sp. nov. A	P77019
<i>Schizophoria</i> sp. nov. B	P77061
<i>Cymostrophia</i> sp. nov.	P77078
Douvilliniid gen. nov.	P1474
<i>Strophonella</i> sp. nov.	P77076
<i>Gypidula</i> sp. nov.	P77027
<i>Australocoelia</i> sp. nov.	P77032
<i>Gracianella</i> sp. nov.	P77060
<i>Ambocoelia</i> sp. nov.	P77030
<i>Quadrithyris</i> sp. nov.	P77077
Acrospiriferid gen. nov. A	P49241
<i>Howellella nucula</i> sub. sp. nov.	P44432
Acrospiriferid gen. nov. B sp. nov. B	P44458
Acrospiriferid gen. nov. B. sp. nov. B	P44461
<i>Acrospirifer</i> sp. nov.	P77080
<i>Cyrtina</i> sp. nov.	P44503
<i>Cyrtinaella</i> sp. nov.	P49250
<i>Uncinulus</i> sp. nov. A	P12615
<i>Uncinulus</i> sp. nov. B	P14604

FIGURE 6

<i>Isorthis</i> sp. nov.	P77046
<i>Salopina</i> sp. nov. A	P77062
<i>Salopina</i> sp. nov. B	P77051
<i>Strophochonetes</i> sp. nov.	P25439
<i>Strophonella</i> sp. nov. A	P77086
<i>Australocoelia</i> sp. nov.	P77080
<i>Gracianella</i> sp. nov.	P77085
<i>Meristella</i> sp. nov.	P77043
<i>Nucleospira</i> sp. nov.	P77070
<i>Hedeina</i> sp. nov.	P804
Ambocoeliid gen. nov.	P74479
<i>Ambocoelia</i> sp. nov.	P77081
<i>Howellella nucula</i> sub sp. nov.	P44439
<i>Molongia</i> sp. nov.	P77073

FIGURE 7

<i>Salopina</i> sp. nov. B	P77067
<i>Schizophoria</i> sp. nov. B	P77065
<i>Molongia</i> sp. nov.	P77075
<i>Australocoelia</i> sp. nov.	P77066
<i>Meristella</i> sp. nov.	P77069
<i>Nucleospira</i> sp. nov.	P77068
<i>Cyrtina</i> sp. nov.	P44512

SHORT COMMUNICATION

FOSSIL PHOCID SEALS FROM THE LATE TERTIARY OF VICTORIA

The living seals of the Southern Hemisphere are diverse, abundant, and widespread. In contrast, there are few published records of Southern Hemisphere fossil seals, and the most significant of these are recent finds from South America and South Africa. Accordingly, until very recently, discussion of the early history of seals has been based primarily on Northern Hemisphere fossils and discussion of paleozoogeography has been biased because of a lack of southern records. The only fossil seal reported previously from Australia is a skull of the sea-lion *Neophoca cinerea* (Otarioidea—fur seals and sea lions) from the Upper Pleistocene, Queenscliff, Victoria (Gill 1968), which was described originally by McCoy (1877) as a new species, *Arctocephalus williamsi*. Here we present a preliminary report of the discovery of fossil phocid seals (Phocidae—true seals) from Victoria.

THE VICTORIAN SPECIMENS

The recently-discovered Victorian fossils encompass a few diagnostic bones that are held by the National Museum of Victoria (NMV), Melbourne. These include P41759, two fused eroded sacral vertebrae (from Beaumaris; see below); P160399, a relatively complete right temporal (Beaumaris; see Fig. 1); P160433, eight vertebrae and four ribs (Beaumaris) and P160441, an incomplete right temporal (from Hamilton). Another specimen, P16198 (an isolated tooth; Beaumaris) was identified by Gill (1957, p. 181) as the tooth of a squalodontid cetacean, but it may be a phocid incisor. The provenance of none of these specimens is in doubt. All the Beaumaris specimens (see Gill 1957, text-fig. 11, for map) were found as float derived from within or just above a nodule bed at the base of the Black Rock Formation (as defined by Abele *et al.* 1976, p. 241) at Beaumaris (about 37°59'S, 145°03'E), near Melbourne. The age is probably Cheltenhamian, possibly Kalimnan, latest Miocene-earliest Pliocene. The Hamilton specimen, P160441, was found in place in a coquina (Gill 1957, text-fig. 6) within the Grange Burn Formation (as defined by Abele *et al.* 1976, p. 215), near locality 8 of Gill (1957, text-fig. 3) on the Grange Burn (about 37°44'S, 141°55'E), near Hamilton. The age is probably Kalimnan. The Grange Burn Formation is succeeded by basalt that has been dated at

4.46 ± 0.1 m.y. (1. McDougall *pers. comm.* to T. H. Rich; revision of date provided by Turnbull *et al.* 1965), which indicates that the Hamilton specimen is no younger than Early Pliocene.

The temporal (P160399) figured here is identified as that of a phocid seal (following Burns & Fay 1970, p. 379) because the bulla is inflated relatively more than in otariids and because the entotympanic portion comprises at least half of the bulla. The absence of a prominent posterolaterally projecting rounded crest on the mastoid bone indicates that it belongs in the Subfamily Monachinae (see Hendey & Repenning 1972, p. 73). Relationships at the tribal level, however, are not clear yet. Like the South African latest Miocene-earliest Pliocene species *Homiphoca capensis* (Hendey & Repenning 1972), which de Muizon & Hendey (1980) included in the Tribe Lobodontini, the tympanic bulla partly covers the petrosal posteriorly. However, the lip of the mastoid does not overlap the posteroventral face of the bulla as much as in *H. capensis*. Furthermore, the entotympanic is more inflated in the Victorian specimen, the apex of the petrosal is slightly thicker dorsoventrally, and the carotid foramen is not exposed to ventral view at the posterior of the bulla. The significance of these and other features is uncertain at present. Determination of relationships at the tribal level and below must await detailed comparison with *Homiphoca capensis*, many other nominal species of fossil phocids (e.g., those mentioned by Ray 1976, de Muizon 1981), the extant species. The temporal from Grange Burn, near Hamilton (P160441, not figured here) lacks the entotympanic and the anterior of the petrosal. There are minor differences in ventral topography with P160399, so that at this stage it is not clear whether they are conspecific. Further work is needed in order to determine whether the remaining taxonomically less informative specimens (vertebrae, ribs, and incisor) are those of phocids or otariids.

SIGNIFICANCE

Phocid seals generally have a poor fossil record, and many details of their evolution are uncertain. The Victorian specimens are important because they provide the first positive pre-Pleistocene record of southern phocids outside Peru, Argentina, and the tip of South Africa. Previously-described



Fig. 1—Right temporal bone of phocid seal from Beaumaris, NMVP160399, X1. Left, dorsal view. Right, ventral view.

southern fossil phocids include: *Homiphoca capensis* (Hendey & Repenning 1972), latest Miocene-Early Pliocene, South Africa (see also de Muizon & Hendey 1980); *Piscophoca pacifica* de Muizon 1981, Early Pliocene, Peru; and *Acrophoca longirostris* de Muizon, 1981, Early Pliocene, Peru. The Victorian specimens are of similar age to the above, but, because their relationships are still uncertain, it is possible to say little about their zoogeographic significance. They at least fill in what was formerly a large gap in the distribution of southern fossil phocids. Their presence relatively further south than any other known southern phocid suggests that the true seals may have colonised circum-Antarctic waters before the Early Pliocene (see also de Muizon 1982, who mentioned the Victorian record based on information from R. E. Fordyce). Further Australasian finds are anticipated.

ACKNOWLEDGEMENTS

We thank J. D. Campbell, John A. Long, Ch. de Muizon, and T. H. Rich for discussion and/or reviewing the manuscript.

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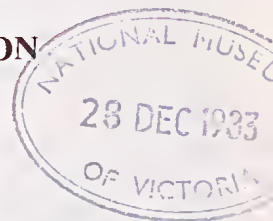


Barren ground, typical of severely salinised flats and lower slopes, is widespread in virtually all but mountainous, high rainfall parts of Victoria. Sheet wash of topsoil and groundwater discharge in erosion gullies, adding sediment and salt to water supplies, are associated with dryland salting. Grassy islands carry a variable cover of valueless *Hordeum maritimum*.

DRYLAND SALINITY SYMPOSIUM—INTRODUCTION

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Throughout history, secondary salinisation (i.e. salinisation induced by particular landuse practices) has resulted in declining agricultural productivity and even total crop failure. In the case of irrigation-related secondary salinisation, water which is deliberately added to the soil is often in excess of plant requirements and percolates downwards to fill the available groundwater storage, causing watertables to rise. Dryland secondary salinity, on the other hand, results from reduced plant water usage which follows the replacement of forests by mainly annual pasture or by certain cropping systems, especially those which include long fallow in the rotation (Jenkin 1979, 1981, Peck 1977).

At the same time, the existence of natural salting should not be overlooked and it is important to distinguish between primary and secondary salinisation. However, there is abundant evidence, particularly in the Victorian Mallee, and the Western Australian wheat belt of man-induced reactivation or spread of natural salinas. In Victoria, most areas of primary salinisation are groundwater discharge areas (Lawrence 1975). Nevertheless, there are large areas of inherently saline subsoils, particularly in inland Australia which, when exposed by the erosion of the topsoil, form salt scalds (Working Party on Dryland Salting in Australia 1983).

The emergence of saline groundwater at the surface produces a salt seep (Peck 1978). There have been many attempts to classify seep phenomena, but none is entirely satisfactory. In this symposium, the word seep is used to cover all secondary groundwater discharge areas despite their variation of form in detail. Besides soil salting, although genetically related to salt seepage, is the increased salinity of surface and groundwaters. Although this is very difficult to quantify, there are numerous cases where it has become significant, not only to individual landholders but also to large communities such as Perth.

Dryland seepage salting is widespread in south-western, southern and eastern Australia, on the Great Plains of North America and in recently-cleared areas of south-east Asia and central America. Thus, the regions affected vary widely in both climate and physiography. Within each area there is some variation in expression, depending on geological structure, topography and climate. In this regard, Victoria appears to be the most variable of all (Jenkin 1981).

In Western Australia, the first concern was in the early 1920s where water used for steam locomotives was becoming noticeably more saline (Wood 1924). It was also recognised that the increasing salinity levels cor-

responded with the area cleared for agriculture, although it was probably J. G. Robertson, a grazier in western Victoria who, in a letter to Governor La Trobe in 1854, was the first in Australia to relate seepage salting to clearing and overstocking. As far as is known, this is the first record anywhere of such an event.

At first, dryland salting in agricultural areas was regarded as a relatively superficial phenomenon. Rain-water infiltrating the soil and moving downslope as soil throughflow was supposed to carry dissolved salts with it and eventually emerge on the valley floor where the salts were concentrated (Cope 1958). However, later work showed that discharge of deeper groundwater was the main factor, although the details of the systems operating were only partly known (Bettenay *et al.* 1964, Jenkin & Irwin 1976, Macumber 1969, Peck 1978). More recently in Australia, research has been concentrated on an attempt to determine the processes involved and to define more clearly the mechanisms operating, particularly in Western Australia, Victoria, South Australia and Queensland. This has met with considerable success and there is now every confidence that the principles involved in secondary salinisation are known.

There are, however, wide variations in detail and the stage has been reached in which it is necessary to "characterise" individual areas or regions. This includes determining and mapping the hydrogeological, geomorphic and soil characteristics of an area so that zones of different groundwater recharge potential can be isolated. The resulting synthesis is then compared with the current landuse map and a management prescription developed for the area. This is designed to maximise water usage by plants and, ideally, to increase agricultural productivity. However, these plans are subject to periodic modification in response to demand and to other factors such as drought. The scales involved vary from quite small hydrological systems which can be treated locally, through regions in which relatively large areas must be treated simultaneously to be effective, to major sedimentary basins in which the recharge area may be far distant from the surface discharge sites, making control extremely difficult.

In this Symposium, different research approaches into the processes and mechanisms involving dryland salinisation, on both local and regional scales, are examined. Further, salinity control involves land management, of the recharge areas as well as the affected sites. The biological aspects of this are also considered. However, although control through the use of suitable plants and appropriate management is likely to dominate the attack on dryland salinity, engineering methods may be important in some areas, particularly in the collection and safe disposal of runoff and the drainage of wet sites and salt seeps.

Salinity affects the community in various ways, from individuals to large groups of the population. There are several aspects to this. Loss of income, falling property values, increasing costs and landscape deterioration are all involved, and the social consequences can be quite significant in the worst-affected areas. Only some of

these socio-economic problems are covered, an indication that herein lies an important field for investigation.

As shown by the papers in this Symposium, dryland salting is a highly complex phenomenon and, to many people, a serious problem. In Victoria, the technical aspects of dryland salinity amelioration are far more complex than elsewhere, a wide range of scales and hydrogeological conditions being involved. As a consequence, solutions, although similar throughout in broad principle, must nevertheless be varied in detail from one salinity province to another. The first requirement then, is to determine the characteristics of each province in some detail. For the next step, which is to prescribe appropriate land management systems, a detailed knowledge of plant-water-soil relationships is essential. Thirdly, the social and economic effects of dryland salinisation are only now starting to be fully appreciated by the community at large. It is probably the water quality aspect which will affect most people directly. This is an area in which further intensive research is needed and it may be that radical departures from traditional agricultural and water supply practice will be necessary. Finally, wide acceptance of the management proposals and concerted action by landholders and government is essential for the effective control of dryland salting.

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THE APPLICATION OF SALT AND WATER BALANCES TO QUANTIFY CAUSES OF THE DRYLAND SALINITY PROBLEM IN VICTORIA

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ABSTRACT: The magnitude of the effect of land use changes applied by agricultural development to the cycles of salt and water are examined using a mass balance model approach. Historical data sets for catchments in the northern slopes of Victoria are used to obtain an estimate of the increase in groundwater recharge. For catchments with recognised soil or stream salinity problems the recharge increase is about 20 mm yr^{-1} ; catchments with water-logging problems have a recharge increase in the range 20 to 80 mm yr^{-1} . These increases are a relatively small proportion of rainfall and similar in magnitude to increases in other parts of southern Australia with similar problems. The characteristic time for equilibration of salt input and loss is of order 1000 years in salt-affected catchments. A mass balance for the 4183 km^2 highlands segment of the Loddon River to Laanecoorie Weir suggests that increased recharge in non-irrigated agricultural land has contributed $60 \times 10^6 \text{ m}^3 \text{ yr}^{-1}$ of water to the development of current groundwater conditions in the Loddon Plain.

Where the mass balance approach is inappropriate, simple equilibrium recharge/discharge models may be useful, particularly as a first approximation, even when empirical estimates of evaporation are included. Discharge estimation using the groundwater flux to the seepage area is preferred when the soil surface is not continuously wet. This method gave an estimate for average recharge of 17 mm yr^{-1} for a salt-affected catchment near Kamarooka.

In southwest Victoria about 50% of mean stream discharge is brackish or saline. In the Wannon River basin, an analysis using a published data set showed that catchments dominated by agricultural land use exceeded forested catchments in salt loss by a factor of 4. Historical data sets appear to be available which, if used in the mass balance approach, could provide an estimate of the increase in recharge for catchments in the southwest region. An advantage of the mass balance approach is that a reasonable approximation can be obtained fairly quickly of the quantities of water and salt involved in recognised processes. This allows the relative importance of each process to be determined as a guide to development of reclamation strategies.

The hydrologic cycle provides a conceptual framework in which the dynamic processes associated with input, transfer and output of water in an environmental system can be analysed. The water cycle transports salts as the solute load in the various phases of the cycle. In natural systems the flows of water and salt are usually steady state flows, at least in a time scale of order 1000 years. The consequence of man's activities, particularly by making drastic changes in land use, is to inject a perturbation into the natural regime which may require a time scale of tens to thousands of years for a new steady state flow condition to be achieved. In most cases it is expected that the re-establishment of steady state flow will have a longer time scale for salt than for water due to the differences in storage characteristics.

The dryland salinity problem has been recognised as a consequence of man-induced changes in the magnitude of some components of the hydrologic cycle. Even if not fully understood, the dynamic nature of the problem is recognised through the observation that the area of salinised land is increasing in practically all locations.

The need to quantify the magnitude of the induced changes in the hydrologic cycle has motivated a number of studies in southern Australia in recent years. The objective of one such study in the Northern Slopes of Victoria during 1981 was to quantify the principal mechanisms of secondary salinisation as a basic require-

ment for establishing criteria for reclamation strategies. This paper indicates the magnitude of changes to components of the hydrologic cycle consequent to agricultural development. Details of the methods used in the study are reported elsewhere (Williamson 1983). As a corollary, it is intended to demonstrate that conceptually simple models can be useful in establishing the order of magnitude of the causes of dryland salinity problems.

THE HYDROLOGIC DISTURBANCE

The hydrologic regime existing in Australia before European settlement had probably achieved steady-state conditions following the major climatic change about 6000 years B.P. Agricultural development has provided a major perturbation to that pristine system (Holmes 1971). The development of a saline seep involves a transient increase in salt loss. If no further land use changes are made, the rate of salt loss could be expected to decay to the pristine level at equilibrium with the rate of salt input from atmospheric deposition and rock weathering processes. The deterioration of water quality in rivers and the secondary salinisation of soils are examples of the consequence of the adjustment necessary to achieve a new steady state. By determining the nature and magnitude of the perturbation applied by agriculture to the cycles of water and salt, it is possible to examine whether the perturbing factors may be altered either to their magnitude under the pristine condition or to a level

which places an acceptable impact on the environment as the new steady-state condition establishes. In the latter case, a significant factor would be the extension of the transient flow phase.

The qualitative description of the causes of secondary salinisation following agricultural development was first published in Victoria over 20 years ago (Cope 1958) and in Western Australia over 60 years ago (Wood 1924). It is only in the last 10 years that studies have adequately quantified the problem (e.g. Peck & Hurle 1973) to allow a rational approach to be made in establishing reclamation strategies.

From the qualitative understanding, it has been established that secondary salinisation requires a source of soluble salt, a source of water, and the mechanism for redistribution of salt. The importance of the groundwater system and the changes applied to it by agricultural development have been recognised through the association of groundwater seepage with salinisation (Williamson & Bettenay 1979, Jenkin 1981).

Consequently, change in groundwater recharge and mass of stored salt which may be redistributed in the regolith need to be quantified. Factors requiring quantification to establish the mechanism for salt redistribution include increase in the leaching rate of stored salt and characteristics of the solute flow and flow path in aquifers. Changes in hydraulic gradient, changes in cross-sectional area of groundwater flow (though not necessarily associated with a change in solute flux), and structural changes of the solute flow path such as in the development of preferred channels following root decay, may contribute to an increase in seepage. An estimation of the increase in groundwater recharge may be made by determining the difference in the sum of evaporation plus surface run-off for pre- and post-development phases. However, using any of the currently available methods for quantifying catchment-scale evaporation, the error term for the estimate of groundwater recharge could be of the same magnitude as the recharge itself. It is preferable, therefore, to make a direct measurement of recharge or of a response by the groundwater system to the change in recharge such as increased discharge or groundwater level change.

APPLICATION OF A MASS BALANCE MODEL

Simple models applying the water balance principle may provide an estimate of recharge to an aquifer system. Results obtained are sensitive to the relationship of actual to potential evaporation, and when comparing changes in land use, the effect of these changes on surface run-off. More sophisticated models which use explicit mathematical descriptions of the hydrologic processes in a catchment are a significant improvement on the simple model for quantifying unknown fluxes such as recharge. Aston and Dunin (1980) achieved an estimate of annual streamflow with an error of 10% using the distributed hydrologic model SHOLSIM. However, the application of these models in many problems is limited by the inability to satisfy their data needs. The historical data sets acquired in the course of routine

monitoring of basic hydrologic characteristics by government agencies, and the compliance type data, though simple and often incomplete, do present a data base often appropriate to use in simpler models.

The combination of the conservation equations for both salt and water provides a set of equations which lead to the determination of the groundwater discharge in a catchment for pre-clearing and present land use conditions. The method is given in detail by Williamson (1983) and follows closely that used by Peck and Hurle (1973). Essentially, salt concentration of present groundwater discharge to a stream is determined by a mass balance analysis of streamflow in which available data are measured values for streamflow volume and salt concentration, an estimate for groundwater discharge volume, and salt concentration of surface run-off. Determination of the pristine groundwater discharge uses a simple mass balance where salt input by rainfall equals salt output by run-off and groundwater discharge. If it is assumed that the salt concentration of groundwater discharge is two or more orders of magnitude larger than the salt concentration of run-off, and that pristine run-off volume is a small proportion of the rainfall, it is possible to obtain an estimate of pristine groundwater discharge using a mass balance equation. Average saltfall in rain is assumed to be the same for both pristine and current land use periods. The salt concentration of groundwater discharge determined for the present agricultural condition is assumed also to be unchanged from the pristine situation. Groundwater discharge from unit area of agricultural land may be estimated given the fraction of the catchment having that type of land use. Groundwater recharge and discharge are equated by assuming that equilibrium conditions for waterflow in the catchment have been achieved where agricultural development commenced over 50 years ago. It is not axiomatic that saltflow from the catchment has reached a steady-state also.

The mass balance model uses available historical data for quantity and quality of rainfall and streamflow (run-off plus groundwater discharge). In addition a number of assumptions other than those already mentioned, must be applied: 1. The annual groundwater discharge component of present streamflow may be estimated as the summation of monthly baseflow using daily rainfall and streamflow records in a simple baseflow separation approach. The method tends to underestimate total groundwater discharge by not making any allowance for evaporation from the stream during summer or enhanced discharge associated with rainfall events. The error is unlikely to exceed 25% when calculated concentrations of groundwater discharge are compared with measured concentrations of streamflow during periods of low flow or of groundwaters in the few boreholes near surface drainage lines. 2. The deep drainage component of the water balance is assumed to be zero, the salinity of run-off is assumed equal to rainfall salinity and, in the pre-clearing situation, rainfall salt input is equated to salt output in streamflow. It is also assumed that the annual salt contribution from

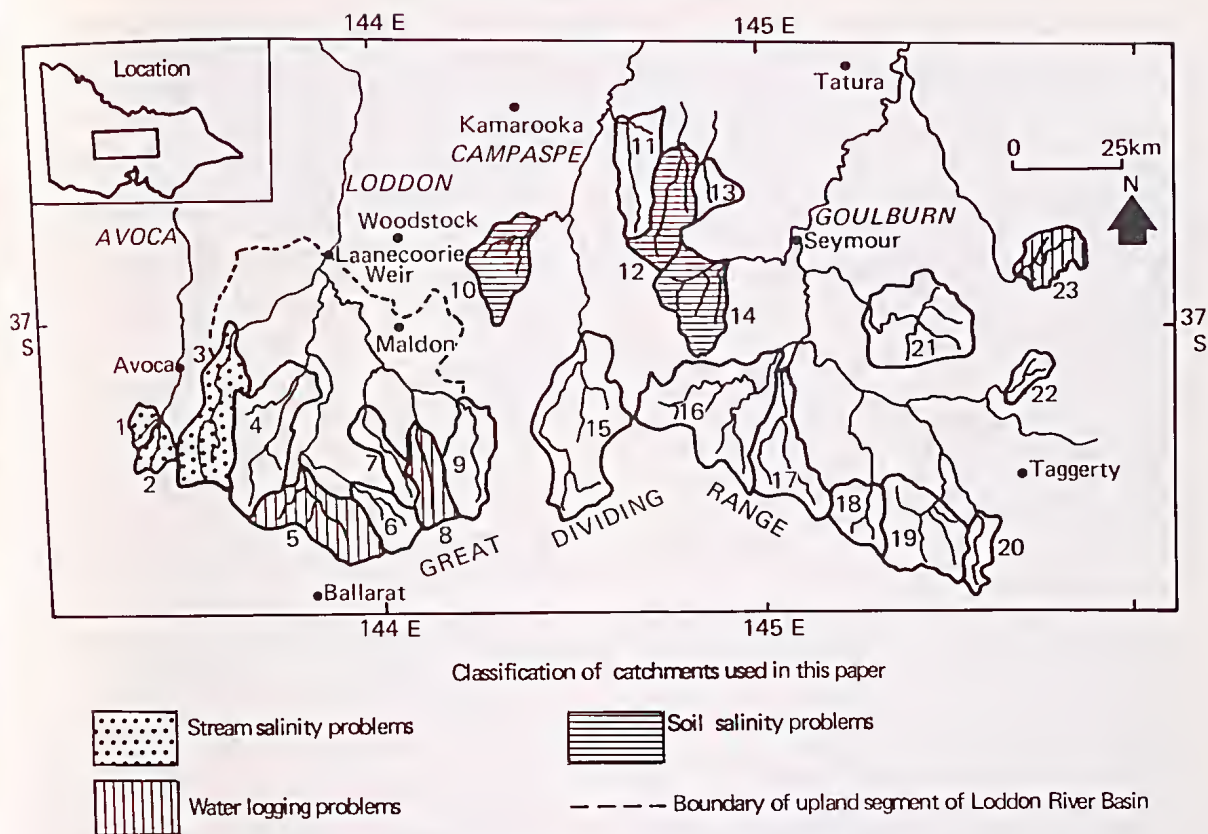


Fig. 1—Location of catchments used in mass balance studies.

weathering of country rock is negligible compared with salt input by rainfall. Salt storage was determined using a trapezoidal integration of salt content for discrete samples over the total depth (usually to country rock) of the sampled profile.

The chloride ion concentration was used as the measure of salinity, primarily because circulation of the ion in the hydrologic cycle is largely through physical processes (Hem 1970). For streamflow, chloride concentration was determined by correlation with electrical conductivity, the correlation coefficients exceeding 0.98 for the 4 major streams for which data were available.

This mass balance model does not pretend to achieve any real depth in conceptualising the hydrologic system as it responds to the change in land use. Further application of the understanding of processes which cause the changes in groundwater recharge and discharge, both in space and time, should be fruitful in developing a more dynamic model which nevertheless avoids the data demands and computational extent of many deterministic models. Despite the simplifying aspects of this model, a measure of average response is achieved even if no dynamic characteristics are elucidated.

CATCHMENT RECHARGE

The mass balance model was applied to 23 catchments within the Goulburn, Campaspe, Loddon

and Avoca River basins shown in Fig. 1. Data on stream-flow quantity and quality were supplied by the State Rivers and Water Supply Commission for the 16 year period from 1965 to 1980. Chloride input in rainfall was estimated using a correlation with distance from the coast in a south-west direction which was established using a data set obtained during a statewide sampling program between 1974 and 1977 by the Department of Agriculture. Land use was determined from Land Conservation Council Maps, and median rainfall isohyets were drawn using rainfall station records of the Bureau of Meteorology which exceeded 50 years duration. The Department of Minerals and Energy core sampling activities provided samples of 36 bore holes for salt storage determination. Results of soil salt contents to about 6 m obtained by the Soil Conservation Authority in several catchments supplemented and supported the deeper borehole data.

The catchments are all within the uplands between the alluvial plain in the north and the Great Dividing Range to the south (see Fig. 1). This is a medium winter rainfall zone, the median rainfall decreasing from 1500 mm yr⁻¹ in the southeast to 450 mm yr⁻¹ in the northwest of the region, and pan evaporation increasing from 1000 mm yr⁻¹ in the south to 1500 mm yr⁻¹ for the most northerly catchments. The general climatic description is Mediterranean type, 77% of the rainfall

TABLE 1
RAINFALL, STREAMFLOW AND CALCULATED GROUNDWATER DISCHARGE FOR CATCHMENTS DOMINATED BY HIGH STREAM SALINITY, SOIL SALTING AND WATER LOGGING PROBLEMS (RESPECTIVELY) IN THE NORTHERN SLOPES OF VICTORIA

Flow and discharge data are averages for 1965-1980 period.

Catchment		Land Use ¹	Rainfall mm yr ⁻¹	Streamflow mm yr ⁻¹	Groundwater Discharge to Streams (mm yr ⁻¹)			Seepage Increase for Agric. Land mm yr ⁻¹
No	Name				Present	Pre-clearing	Agric Land	
1	Glenlogie	1.0	620	73	22	2	22	20
2	Amphitheatre	0.9	660	58	16	2	18	16
3	Norwood	0.9	580	59	7	1	8	7 ²
10	Axe Creek	0.7	650	69	13	1	19	17
14	Major's Creek	0.5	570	59	5	1	9	8 ²
12	Colbinabbin	0.8	530	45	3	1	4	3 ²
5	Clunes	0.8	720	85	25	9	29	20
8	Yandoit	0.6	850	158	50	17	77	60
23	Polly McQuinn	0.9	990	318	141	69	149	80

¹ Data are the proportion of the catchment cleared for agriculture.

² Catchments where the output of water from the catchment by groundwater flow beneath the stream gauging station is considered an important factor though estimated to be less than the groundwater discharge component in streamflow.

occurring in the May to October period resulting in a cool wet winter and a hot dry summer.

Results of the calculated groundwater discharge component of streamflow for pristine and present land use conditions in a number of catchments are given in Table 1. The table is in three sections representing catchments with stream salinity (Catchments 1, 2, 3), soil salinity (Catchments 10, 12, 14) or water-logging (Catchments 5, 8, and 23) problems associated with the development of more than half the catchment for agriculture. For 3 catchments (3, 12, and 14), the subsurface groundwater discharge is considered to be an im-

portant contribution to total groundwater discharge. Data are not available to calculate the contribution. Using estimates of the magnitude of the hydraulic parameters it is suggested that subsurface groundwater discharge from any of the catchments will be less than the groundwater discharge via streamflow, even where deep leads are involved.

The seepage increase for the agricultural land segment of each catchment is the measure of groundwater recharge increase due to agricultural development. For the 6 catchments with recognised soil or stream salinity problems associated with dryland agriculture, recharge

TABLE 2
SALTFLOW, STREAM SALINITY, SALT STORAGE AND CHARACTERISTIC TIME TO EQUILIBRIUM FOR SELECTED CATCHMENTS IN THE NORTHERN SLOPES OF VICTORIA

Flow and salinity data are averages for 1965-1980 period.

Catchment		Present Stream Salinity mg Cl ⁻ L ⁻¹	Saltflow in stream g Cl ⁻ m ⁻² yr ⁻¹	Saltflow to Saltfall ratio	Estimated Mean Salt Store g Cl ⁻ m ⁻²	Net Salt Loss g Cl ⁻ m ⁻² yr ⁻¹	Characteristic Time to Equilibrium years	Stream Concentration at Equilibrium mg Cl ⁻ L ⁻¹
No	Name							
1	Glenlogie	455	34	13.4	No data	31	—	34
2	Amphitheatre	448	26	10.4	No data	24	—	43
3	Norwood	258	16	6.5	23 × 10 ³	13 ¹	1200	40
10	Axe Creek	276	19	10.0	32 × 10 ³	17	1700	28
14	Major's Creek	134	8	4.5	No data	6 ¹	—	32
12	Colbinabbin	151	7	3.8	22 × 10 ³	5 ¹	2700	40
5	Clunes	94	8	3.0	2 × 10 ³	5	60	32
8	Yandoit	47	7.5	3.1	2 × 10 ³	5	300	15
23	Polly McQuinn	11	3.5	2.2	No data	2	—	5

¹ Does not include salt loss in subsurface drainage, which if included, would reduce the characteristic time to equilibrium.

increase is of order 20 mm yr^{-1} . This is about 3% or less of the median annual rainfall, and about 1% of the annual average pan evaporation. For the catchments with water logging problems, the estimated recharge increase due to agriculture is in the range 20 to 80 mm yr^{-1} , being up to 8% of either median annual rainfall or average annual pan evaporation. In the Polly McQuinn catchment, the seepage-induced water logging is particularly noticeable even at quite high positions in the landscape. Nevertheless, in all cases, the increase in recharge following agricultural development is a relatively small proportion of the rainfall, and is in the range of estimates given for interception difference between forest and grassland (Blake 1975, Holmes & Wronski 1981). The range of recharge increase is similar to that obtained by Peck and Hurle (1973) of from 23 to 65 mm yr^{-1} in a similar rainfall range in southwest Australia. In southeast South Australia drainage measurements using a lysimeter (Holmes & Colville, 1970) and a steady-state environmental chloride and tritium concentration method (Allison & Hughes 1978) gave results for mean recharge in the range from 50 mm yr^{-1} for a sand over heavy clay to 250 mm yr^{-1} for free draining skeletal soils all vegetated by improved pasture. Allison and Forth (1982) have estimated that the present day recharge in southeastern South Australia is approximately 2.5 times the pristine levels.

SALT BALANCE AND EQUILIBRIUM TIME

The average (flow-weighted) stream salinity for the 1965-80 period (Table 2) reflects the effect of agriculture on stream water quality. The saltflow to saltfall ratio indicates that there is a net export of salt from all catchments. It is a characteristic of catchments with salinity problems that the output/input ratio for salt exceeds 5 when an estimate of the subsurface saltflow component is included in the salt output.

The characteristic time to equilibrium is the time taken for the enhanced groundwater discharge rate to decrease the salt store in the regolith to a new equilibrium level, identified by the re-establishment of a balance between salt input and output. Assuming that the present saltflow conditions are maintained, the characteristic time to equilibrium for catchments with salinity problems is of order 1000 years (Table 2). For the catchments with waterlogging problems, the characteristic time is less, being a period of tens to hundreds of years. At equilibrium the salt concentration of streamflow would be lower than for the pristine environment due to a higher volume of stream flow in the new equilibrium state. Peck & Hurle (1973) estimated characteristic times of order 100 years for catchments with dryland salinity problems in southwest Australia.

The results obtained in the northern slopes catchments suggest that an average salt storage greater than $20 \times 10^3 \text{ g Cl}^- \text{ m}^{-2}$ is a characteristic of the regolith in catchments with dryland salinity problems (Table 2). The thickness of weathered material above the country rock is in the range 10 to 100 m for the 36 sampled boreholes located either within or adjacent to catch-

ments used in the study. The basalt profiles (dominant in Clunies) contain the lowest salt storage except when they overlie siltstones, slates or weathered granites which probably restrict drainage and promote salt accumulation. The higher salt storages are associated with the alluvial profiles (usually clay) and Silurian mudstones. There is a general increase in stored salt with decreasing rainfall indicating a degree of climatic control. The salt storage is similar in magnitude to that found in southwest Australia where the range is from 6×10^3 to $60 \times 10^3 \text{ g Cl}^- \text{ m}^{-2}$ for a rainfall zone from 1400 to 500 mm yr^{-1} (Stokes *et al.* 1980). The importance of quantifying salt storage for the full depth of the weathered profile becomes obvious when the hydrologic significance of seepage from aquifers in the weathered zone is accepted as the primary process in dryland salinisation (Jenkin 1981). The salt stored in the arable surface zone (to say 1 m), even if saline conditions have established, is unlikely to exceed 5% of the total profile salt storage.

REGIONAL MASS BALANCE—LODDON RIVER DRAINAGE BASIN

Seven catchments in the study set occupy 1880 km^2 in the upland segment of the Loddon River basin which forms the catchment to Laanecoorie Reservoir (Fig. 1). Numerous branches of the Loddon Deep Lead trunk system occur within the catchment and converge at a point about 11 km northeast of Laanecoorie Weir before continuing under the Loddon Plain. The drainage by the lead system should be included when quantifying the water and salt balance for the upland region. Data given by Macumber (1978b) on the dimensions and hydraulic conductivity of the trunk lead system near Woodstock, and an assumed hydraulic gradient of 0.01 were used to calculate the waterflow in the lead from the upland catchment. The portion of this flow which originates in the Avoca basin is unlikely to be greater than 25% if the cross-section of this tributary lead is used as the basis of estimation. The salinity of the groundwater is of order $1000 \text{ mg TDS L}^{-1}$ (about $350 \text{ mg Cl}^- \text{ L}^{-1}$) near Bridgewater (Macumber 1978a).

Average annual saltflow and waterflow for the 4183 km^2 catchment to Laanecoorie Weir have been determined for the period 1965-1980, and are given in Table 3. The estimate of saltflow and waterflow contributed by the lower segment of the catchment is obtained by difference, assuming that the river is not influent to the groundwater system, between the upper segment and Laanecoorie Weir. The regional mass balance quantifies the contribution by agricultural land use in the highlands to streamflow and aquifer development in the Loddon Plain.

The results in Table 3 also show that the deep lead system contributes about 10% of the waterflow from the highlands to the plain, but about 25% of the salt. The salt input to the catchment in rainfall is estimated at $2.3 \text{ g Cl}^- \text{ m}^{-2} \text{ yr}^{-1}$ to give a saltflow to saltfall ratio of 3.7 , indicating that there is a net export of salt from the highlands to the plain. The salt loading delivered to the

TABLE 3
SALT AND WATER FLOW FOR THE CATCHMENT OF THE LAANECORIE RESERVOIR WHICH FORMS THE
HIGHLANDS SEGMENT OF THE LODDON RIVER DRAINAGE BASIN

	Area km ²	Waterflow		Saltflow	
		m ³ yr ⁻¹	mm yr ⁻¹	tonnes Cl ⁻ yr ⁻¹	g Cl ⁻ m ⁻² yr ⁻¹
SURFACE WATER SYSTEM					
Upper Segment (7 catchments)	1880	167 × 10 ⁶	89	16.5 × 10 ³	8.8
Lower Segment	2303	59 × 10 ⁶	24	10.4 × 10 ³	4.5
Whole Catchment	4183	226 × 10 ⁶	53	26.9 × 10 ³	6.4
DEEP LEAD SYSTEM					
Flow at Woodstock	4183	25 × 10 ⁶	6	8.7 × 10 ³	2.1
COMBINED SURFACE AND DEEP LEAD SYSTEMS					
Total	4183	251 × 10 ⁶	59	35.6 × 10 ³	8.5

plain as a consequence of man's activities is about 26×10^3 tonnes Cl⁻ yr⁻¹ (about 73×10^3 tonnes TDS yr⁻¹).

An average recharge increase for agricultural land of 21 mm yr⁻¹ has been calculated using the mass balance model for the 7 catchments forming the upper segment, and is equivalent to 29×10^6 m³ yr⁻¹. The streamflow records at Laanecorie Weir cannot be used to estimate the groundwater discharge to the stream due to the effect of the reservoir on the stream hydrograph. The stream quality data show an average concentration during low flows of about 400 mg Cl⁻ L⁻¹. This was used in the Peck and Hurle (1973) version of the mass balance model to obtain an estimate for average recharge increase of 18 mm yr⁻¹ to the 3292 km² of agricultural land in the Laanecorie catchment. This is equivalent to 59×10^6 m³ yr⁻¹. Therefore the average recharge increase for agricultural land in the lower segment is about 16 mm yr⁻¹, equivalent to 30×10^6 m³ yr⁻¹. This is accepted as a reasonable estimate. Further, it can be shown from the simplified pristine mass balance that the estimate for pristine groundwater discharge is about 4 mm yr⁻¹ or about 17×10^6 m³ yr⁻¹ which is 70% of the present estimate for flow in the trunk deep lead.

These results suggest that there is a groundwater contribution of about 60×10^6 m³ yr⁻¹ by agriculture to the flow from the highlands to the Loddon Plain. As a natural drainage system, the trunk deep lead is apparently functioning at maximum capacity, with the balance of the increase in recharge (about 35×10^6 m³ yr⁻¹) becoming output to the surface drainage lines. The contribution that this excess water from the highlands may have on salinisation of non-irrigated farmland in the Loddon Plain is dependent on the geohydrologic features which may direct flow toward the soil surface along preferred channels or provide conditions for development of extensive areas of shallow groundwater. Irrigated agriculture has been considered to be a signifi-

cant contributor to the development of the current groundwater conditions in the Loddon Plain (Macumber 1978b). The mass balance results suggest that increases in recharge due to non-irrigated agriculture in the highlands should be considered also as an important source of water and salt for the development of groundwater problems in the Loddon Plain.

A SIMPLE EQUILIBRIUM RECHARGE-DISCHARGE MODEL

The assumption of a steady-state flow condition for water in a catchment provides a basis for estimating average recharge. Particularly in catchments with low relief, the loss of water by evaporation from saline seepages can be expected to dominate and exceed the discharge to a stream. Use of the combined salt and water balance model may be quite inappropriate or may be limited by a lack of a reasonable length of a stream flow record as in the case of catchments 11, 12 and 13.

The water balance condition that discharge equals recharge assumes that the steady-state has been achieved following the hydrologic perturbation applied by agricultural development. Having established the area of the groundwater discharge zone (A_d), the area of recharge (A_c) can be assumed to be that part of the catchment which is not a discharge zone. The average recharge (R_c) is given by the simple equation

$$R_c = \frac{A_d G}{A_c}$$

The groundwater discharge (G) may be estimated as the sum of seepage flow (F_x) to a stream and evaporation from the seep area (E_s) estimated as a fraction (f) of pan evaporation (E_p). Alternatively, the discharge (G) may be estimated using the physical characteristics of the flow path of groundwater to the seepage surface in an appropriate flux equation.

Where there is no apparent seepage flow across the soil surface, care is needed in the assumption that evaporation from the discharge area is at the potential rate. For any particular seepage area, use of evaporation from the seep, horizontal flow to the seep in the groundwater system, and an analysis of vertical flow to the seepage area, provide independent checks on the estimate of average current discharge.

This input-output model was used to estimate the recharge for a catchment of 2090 ha near Kamarooka. A saline seepage zone of 390 ha has developed at the upland edge of the alluvial plain, the recharge area being in gentle hills formed on Ordovician sedimentary bedrock strata (Dyson & Jenkin 1981). This system contains aquifers in the weathered zone at 15 to 20 m depth and in an underlying less weathered fractured and jointed zone. Within the saline seepage zone, piezometer nests indicate that the gradient for flow is toward the soil surface. The deeper jointed aquifer appears to be the primary flow path for water from the recharge area to the seepage area. There is no defined surface drainage line associated with the saline seepage area.

To use the evaporation approach to estimate recharge, the following parameter values were obtained: $A_s = 390$ ha, $A_c = 2090 - 390 = 1700$ ha, $F_s = 0$, $E_s = 0.6 E_p = 0.6 \times 1350 = 810$ mm yr^{-1} , leading to the annual recharge estimate of 185 mm.

The hydraulic properties of the seepage area provide an alternate data set. The vertical flow path includes an alluvial clay zone whose average hydraulic conductivity is known (0.01 m day^{-1} , see Dyson & Jenkin 1981). The piezometer nests provide measurement of the average hydraulic gradient (0.02). Applying Darcy's Law, the discharge flux density for the seepage area, G , is 0.073 m yr^{-1} . The estimate of catchment recharge is therefore calculated as 17 mm yr^{-1} with the variation in hydraulic parameters suggesting that the recharge rate lies in the range 10 to 40 mm yr^{-1} (P. Dyson, personal communication). The rainfall for this catchment is 450 mm yr^{-1} which suggests that the recharge estimate of 186 mm, using the evaporation approach, is too large. The

absence of surface flow of seepage water from the saline area and the hydraulic control on the vertical flux of water (Dyson & Jenkin 1981) further suggest that it is inappropriate to use a measure of potential evaporation in this case. The alternate groundwater flux approach provides an acceptable recharge estimate of order 20 mm yr^{-1} .

The application of this input-output model may also be appropriate in areas such as the Mallee. In many situations, the simple approach may provide not only an estimate of recharge, but also a quantification of fluxes in the hydrologic system which would assist identification of the significant flow paths for water and salt.

POTENTIAL FOR APPLICATION OF MASS BALANCE MODELS

Dryland salinity has tended to focus on the consequence for soil resources, with attention given primarily to those catchments adjacent to the River Murray or having tributaries to the river. These have flow of high volume and generally of good quality. In western Victoria, the effect which agricultural development has had on increasing recharge of groundwater results in increased saline seepage to the soil surface and to streams in particular. The loss in quality of water resources usually has a greater economic cost than the degradation of soil resources.

The 9 river basins west of Melbourne and south of the Great Dividing Range contribute 14% of the surface water resources of Victoria. Flow in 3 basins is classified as marginal quality, and in another 4 as brackish or saline (Water Resources Council 1980). About 50% of the mean discharge of 3.3×10^9 m³ yr^{-1} by the rivers exceeds 1000 mg TDS L^{-1} . The Avoca River is the only other river basin in Victoria whose flow is similarly classified (Water Resources Council 1980).

Table 4 provides data comparing the yield of brackish and saline water resources in Victoria with those in southwest Western Australia where the impact of dryland salinisation on water quality is of major con-

TABLE 4
COMPARISON OF YIELD OF BRACKISH AND SALINE WATER RESOURCES FOR VICTORIA AND SOUTHWEST WESTERN AUSTRALIA

Location	Area km ²	Yield of Brackish and Saline Water m ³ km ⁻² yr ⁻¹	Average Total Water Yield m ³ km ⁻² yr ⁻¹
VICTORIA			
South-West Rivers (Basins 30 to 38)	43 900	37×10^3	76×10^3
All River Basins	245 860	7×10^3	95×10^3
WESTERN AUSTRALIA			
South-West Rivers (Basins 3 to 14, 16)	71 200	24×10^3	80×10^3
South-West Coast Drainage Division	314 500	8×10^3	21×10^3

Sources: Water Resources Council, 1980; Brown, 1983.

cern (Sadler & Williams 1981). The 13 river basins in southwest Western Australia have potential for water resource development and lie within 280 km of the coast. The southwest Coast Drainage Division includes the wheatbelt and other intensive agricultural developments in southwest Western Australia. Whilst recognising the difference in geographical factors of the regions being compared, there is significance in the similarity of yields of low quality water resources. The concern for the low quality of about 30% of the water resources in southwest Western Australia has promoted extensive investigations into the causes and management of the salinisation. With 50% of the water resources of southwest Victoria of inferior quality, there is need, apparently, for increased activity in examining the causes and possible management options in the region.

The economic and social impact of degraded surface water resources is diminished when alternative reliable sources, particularly groundwater, are available. Increasing demand on water resources for industrial and domestic use by places such as Geelong and Portland could direct attention to the causes of the poor quality of surface water. In addition to saline seepage resulting from clearing, two major drainage schemes contribute to the salinity of the Barwon River (Gutteridge, Haskins, & Davey 1979). Saline seepage from areas of dryland agriculture has reduced the water quality to stock supply, at best, in all but the more mountainous upper reaches of both the Glenelg and Wannon Rivers (Anon 1968). A survey of the Otway Soil Conservation District has identified 57 km² of salinised soil (J. Duff, pers. comm.) in the Lake Corangamite and Barwon River drainage basins.

Re-working the data for the Wannon River originally presented by Currey (1970), with additional data on land use in each of the 8 catchments examined, provides some quantification of the effect of agricultural land use in the region. For forested catchments, the saltflow to saltfall ratio was 2.4 with mean stream salinity in the range 45 to 100 mg TDS L⁻¹. For catchments dominated by agricultural land use, the saltflow to saltfall ratio was 13 with mean stream salinity in the range 750 to 1500 mg TDS L⁻¹. For the 4500 km² catchment of the Wannon River to Sandford, the salt loading to the river by agriculture was about 140×10^3 tonnes TDS yr⁻¹. Assuming that salt storage was similar to the Northern Slopes, the characteristic time to equilibrium would be of the order of hundreds of years. Land development of 160 km² in the catchment of the Glenelg River above Rocklands Reservoir was not approved following an enquiry in 1968 which estimated that water quality in the reservoir would become unacceptable (Anon 1968).

The historical data sets, providing streamflow quantity and, at least, first order water quality information, appear to be adequate in the southwest of Victoria (AWRC 1978) to apply the mass balance model. It is expected that quantification of salt and water fluxes will confirm that land use change has caused the apparent degradation of the water resources of the region. As for the Northern Slopes, the results should assist in establishing appropriate strategies for reclamation.

DISCUSSION AND CONCLUSIONS

Although the simple water and salt balance approach can provide an interpretation of the consequences of land use change in quantitative terms, and assist in developing criteria for reclamation strategies, more detailed studies are needed to reach a practical and effective control of the increase in recharge. The major advantage of the simpler model approach is that one can obtain fairly quickly a reasonable approximation to the quantities involved in recognised processes. In addition, it is possible to identify the relative importance of each process and establish where more detailed studies should be most effective. For example, the recharge estimate obtained using the simple mass balance model is only an average for the agricultural land in the catchment including discharge areas. Further quantitative studies are needed to identify the variation in recharge rate in a catchment and determine the relative input to total catchment recharge volume of each contributing segment.

It is a reasonable criticism of the models demonstrated in this paper to say that there is unused understanding of the processes in the hydrologic cycle which could be applied to broaden the conceptualisation included in the models. Improvements could include giving the model a two or three dimensional structure, and incorporating concepts which remove the more sensitive but important assumptions. The use of simple models should help to identify the system parameters whose measurement is essential. Further development of the simpler model type should be beneficial for those who have limited data sets or who lack the resources to obtain the intensive data sets for the more sophisticated deterministic or stochastic models.

The effect of agricultural development has been shown to produce an increase in recharge to groundwater of about 20 mm yr⁻¹ where soil and stream salinity problems have developed. With the characteristic time to a new equilibrium in saltflow of order 1000 years, there is need to establish how land management may be modified to reduce the rate of redistribution of salt to surface soils and streams. In the higher rainfall catchments water logging appears to be the significant effect of agricultural development. Though not apparently leading to salinisation, productivity of the land is reduced. The highlands segment of the Loddon River Basin has an average recharge increase also of order 20 mm yr⁻¹ which apparently exceeds the capacity of the natural drainage by the deep lead system. The importance of this contribution to the high water table and salinisation problems in the Loddon Plains needs to be compared with the contribution by irrigated agriculture.

Whilst the problem of soil salinisation associated with dryland agriculture in north and central Victoria has received increasing attention, the effect of dryland agriculture on surface water quality in the southwest of the state appears to have been ignored. About 50% of stream discharge exceeds 1000 mg TDS L⁻¹. Application of the mass balance model could assist in quantifying the cause and providing a basis for determining appropriate management for reclamation.

ACKNOWLEDGEMENTS

Most of the results were obtained using historical data sets provided by State Rivers and Water Supply Commission, Soil Conservation Authority, Department of Agriculture, Victoria, and Bureau of Meteorology. Salt storage data were obtained using core material supplied by Department of Minerals and Energy. The studies on which most results are based were funded by a contract between CSIRO Division of Land Resources Management and the Ministry for Conservation, Victoria. The author is grateful for discussions with many people working on the problem of dryland salinity, but in particular Mr Phil Dyson. Technical assistance in much of the data processing was capably provided by Mrs Lynette Brooks.

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DRYLAND SALTING AND GROUNDWATER DISCHARGE IN THE VICTORIAN UPLANDS

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ABSTRACT: Secondary dryland salinity in Victoria is the result of increased groundwater recharge and discharge post European settlement. The change in ecology produced by the development of agricultural practices has altered the nature of hydrologic balance of groundwater systems. The ability to store water in the regolith has been depleted and groundwater has risen in the landscape. Additional recharge post clearing is now offset by the development of new groundwater discharge sites and increased baseflow of streams.

Increased groundwater recharge and discharge has occurred since clearing of native vegetation and its subsequent replacement with shallow rooted pastures and crops. The decrease in evapotranspiration has allowed profiles to saturate and drain more frequently causing greater accessions to groundwater. Estimates of current mean annual groundwater recharge generally range from 10-50 mm/yr.

The rise and migration of groundwater through the landscape is leaching ions once stored throughout the regolith toward discharge sites where they appear in stream baseflow, or concentrate in the soil producing affected land. Recharge and discharge of groundwater systems may be confined to particular catchments or sub-catchments or may be independent of topography. The nature of the groundwater system depends on geological and geochemical development of the landscape.

Dryland salting is particularly severe and extensive where the pallid zone clays of deeply weathered landscapes are semi-confining to groundwater discharge. Catchments within these landscapes appear to possess a groundwater balance independent of adjacent catchments. Conversely landscapes which do not have a deeply weathered regolith appear to possess groundwater systems of a more regional nature, i.e. independent of surface relief. In either situation it is possible to have landscape components which behave as "preferred" intake zones for groundwater recharge, and the significance of these components needs to be assessed in order to gauge the effectiveness of land use changes designed to ameliorate dryland salinity.

The movement of soluble salts in the landscape depends upon the dynamics of water in the zone of weathering. The addition or removal of water may cause dissolution, dilution, precipitation or leaching, and the dominance of any one of these processes is a function of geological, hydrological, geochemical, vegetative and climatic factors. In response to these factors, hydrological conditions developed which tended to store salts within the unsaturated regolith. This was achieved through the agency of native vegetation which maximised water use.

The development of modern agriculture required the removal of native vegetation and its replacement with species possessing different water use characteristics, a change which subsequently produced changes in the hydrological cycle. Saturation and deep drainage beyond the soil and root zones of the upper regolith occurred more frequently and the level of groundwater rose as available storage was depleted. Eventually groundwater reached the surface in the lower landscape, where it now discharges. The groundwater is generally saline because it contains ions leached from the previously unsaturated regolith. The leaching of salts as groundwater migrates toward discharge sites progressively depletes the salt storage of the regolith. Ions may be exported via groundwater baseflow in streams or may concentrate in the soils at the discharge sites.

The environmental effects of saline discharge are increased stream and soil salinity. Soil salinity in discharge areas commonly exceeds that tolerated by common crops and pastures and affected areas frequently become

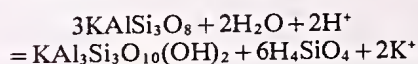
either completely devoid of vegetation or support only the most salt tolerant species.

THE ORIGIN OF SOLUBLE IONS

Water may introduce ions to the landscape through small concentrations in rainfall or by reaction with the minerals in the regolith, releasing ions to solution during the formation of new mineral species.

Ions introduced in the rainfall are believed to be mainly of oceanic origin, contained in the spray produced by the action of wind and waves, although some ions are believed to originate from dust blown up from cultivated soils or from deserts. Ions are progressively removed as they move inland, a general decrease in ionic concentration in rainfall being observed with increasing distance from the coast (Hutton & Leslie 1958). As these ions return to the oceans via overland and subsurface water flow the process as well as the ions involved have been termed "cyclic".

The successive chemical decomposition of both primary and secondary minerals at or near the earth's surface may produce ions in solution. Weathering results in new minerals which are stable within each of a succession of new environments. For instance, the decomposition of orthoclase to muscovite can be expressed as follows:



Thus silica and potassium ions are released to the regolith solution. It is emphasised that the process is not

restricted to the decomposition of fresh primary rock-forming minerals, but continues until equilibrium is established between mineral composition and the hydrological environment (Garrels & Christ 1965).

THE EFFECT OF DEEP WEATHERING

The association of deep weathering and saline areas is well known. Most of the severe salinity problems in Western Australia occur on deeply-weathered igneous and metamorphic terrain (Mulcahy 1978). In Victoria, also there are remnant pockets or belts of deeply weathered bedrock, mostly considered to be residuals of deep Tertiary weathering (Gunn & Richardson 1979). This association of salinity problems with deeply and intensely weathered areas is not the result of continuous release of ions during rock weathering as is sometimes stated. Rather, weathering increases the ability of the regolith to store ions, and rock decomposition and the development of clays and silts increases the ability of deep rooted vegetation to penetrate the regolith allowing evapotranspiration over long periods to produce high ion storage characteristics. Peck (1977) noted high concentrations of ions in the root zone of forests in deeply weathered catchments of Western Australia and considered the phenomena to be the result of ion exclusion by trees during soil water use.

The decomposition of rock forming minerals during weathering could not explain high ion storage because the intensive leaching necessary to form the present minerals (mainly kaolin) indicates that ions produced by such water-primary mineral interactions would have been largely removed by percolating solutions. In addition, the geochemistry of the present waters show that they are in equilibrium with the secondary clay minerals and not the primary rock minerals or their immediate decomposition products. The production of kaolinite and other clays has the effect of reducing permeability and tends to produce confining layers in the system. Groundwater moves through such systems only with difficulty and deeply weathered landscapes all appear to possess steep hydraulic gradients with low hydraulic conductivities in the pallid zone.

Deeply weathered profiles, and associated salinity problems occur extensively along the foothills of the Victorian uplands and on the Dundas Tablelands in the southwest. Drilling in these areas has revealed piezometric surfaces which suggest groundwater systems that converge toward valley floors with very marked groundwater divides coincident with topographic divides. The piezometric surface in the valley floor is commonly above ground surface, and bores tend to be artesian. This groundwater system has developed because of increased recharge following agricultural development and the ability to store groundwater within the system has been exhausted, with recharge on the slopes now approximating discharge on the valley floor. Therefore it is proposed that in the present salt-affected, deeply-weathered catchments annual groundwater discharge is close to being in equilibrium with annual groundwater recharge.

A groundwater and salt balance model has been developed for a deeply weathered catchment at Kamarooka, to the north of Bendigo where the upland front disappears beneath the Riverine Plain. Discharge occurs at the break of slope between the plain and the uplands where the groundwater capillary fringe reaches the surface. This generally occurs where groundwater is present within 1.5 metres of the surface. Further, the groundwater catchment is well defined and coincides with the surface catchment. In this case, approximately 1700 ha of recharge area contribute groundwater to 390 ha of discharge area. Calculations based on upward groundwater gradients within the discharge area suggest a mean annual discharge of approximately 75 mm/yr. Recharge to groundwater was calculated assuming an equilibrium between recharge and discharge and mean annual recharge was found to be approximately 17 mm/yr. Thus, a recharge of only 17 mm/yr in a 1700 ha catchment will maintain a 390 ha discharge area.

BEDROCK AQUIFERS OF THE WESTERN UPLANDS

Although dryland salinity problems are generally common and severe in areas that are deeply weathered they are not confined to these. The problem occurs throughout the uplands and again is a feature of groundwater discharge (Jenkin 1979).

The uplands consist mostly of folded sedimentary rock with a well-developed network of joints and other fractures which permit the transmission of water through otherwise almost impermeable rock (Dyson & Jenkin 1981, Jenkin & Dyson 1982), the significance of fractured rock systems has been pointed out by Legrand (1979), and is a phenomenon which has been considerably underrated in the past although it is fundamental to dryland salting in the Victorian Uplands. Although drilling near Eppalock, southeast of Bendigo, has revealed a regional aquifer system with a piezometric surface of very low relief, the relationship between piezometric surface and catchment topography is not yet well defined. Adjacent catchments have piezometric surfaces at similar elevations but these vary with time in response to rainfall and drought. On a regional basis, the low relief of the piezometric surface in relation to topography suggests a high fracture permeability. In both forested and cleared catchments, piezometric surfaces have been revealed at depths ranging from 10 to 40 m below the ground surface, depending on topography. The forested catchment is approximately 2 km southwest of the cleared catchment and some 30-40 m higher, but the piezometric surface is at about the same level for both catchments, that is 209-210 m above sea level.

The rise in this regional groundwater system is responsible for the present salinity phenomena within the Uplands. The regional groundwater now intersects the lower ground surfaces, where it discharges, salinising land and increasing saline baseflow in streams.

RECHARGE TO FRACTURED ROCK AQUIFERS

The accession of water to regional groundwater systems seems to occur universally throughout the Uplands. However, recent work on the hydrological properties of soils in the region suggests that, while recharge occurs throughout the landscape it may be much lower on the valley floors and lower slopes compared with the upper slopes (Dyson & Jenkin 1981). The former carry duplex soils with a sandy loam about 10-15 cm thick overlying approximately 50-70 cm of medium clay. The clays are sodic leading to the upper B horizon being relatively impermeable, with infiltration rates of about 5 mm/day. The upper slopes and rocky ridges typically have thin, skeletal, uniform or gradational soils which exhibit high, although extremely variable saturated infiltration characteristics (300 mm/day and sometimes greater). It follows that these areas would contribute significantly to recharge if their areal extent within the catchment is sufficiently large. For example, water and salt balance studies of streams throughout northern Victoria suggest that mean annual recharge is between 10 mm/year and 40 mm/year (D. Williamson pers. comm.). These figures are calculated for the catchment as a whole unit and it assumes that recharge is evenly distributed. However, if we partition this recharge for the total catchment between the higher infiltration zones of the upper slopes and the remainder of the catchment, and successively increment recharge in the "critical" area, the sensitivity of this land component can be gauged. The results of this simulation are presented in Table 1 assuming an overall catchment recharge of 20 mm.

Table 1 indicates that the upper slope gradational soils and rocky ridge country may be a critical component in affecting the recharge to regional fractured rock aquifers. Up to 30% of a catchment on the northern slopes of the uplands may consist of this component as a study of the Axe Creek catchment near Bendigo has shown (J. S. Duff pers. comm.). Partitioning calculations based on this figure show that 65 mm of recharge within this area implies less than 1 mm of recharge over the remainder of the catchment. Furthermore, if we accept these recharge figures, this area would be expected to supply 83% of the annual groundwater accession within the catchment.

The presence and distribution of groundwater divides coinciding with topographic divides in these areas has yet to be investigated. There is a dearth of information concerning the fractured rock aquifers of the Uplands, and hydrological characteristics including hydraulic gradients, potentiometric surfaces, storage coefficients and hydraulic conductivity are not yet available. Estimates at present are based on very limited data; thus Plier Malone (1982) considers that gross hydraulic conductivity is probably several metres per day and classical techniques for determining these properties are usually not applicable to fractured rock aquifer systems (Legrand 1979). It is clear that a much better understanding of the groundwater regime of the uplands is essential before land use management systems

TABLE 1
SIMULATION OF SIGNIFICANCE TO GROUNDWATER OF A CRITICAL COMPONENT WITHIN A CATCHMENT ASSUMING AN OVERALL CATCHMENT RECHARGE OF 20 MM/YR

Component area (% of catchment)	Assumed recharge (mm) and groundwater contribution (%)		Recharge in remaining catchment (mm) and groundwater contribution (%)	
	mm	%	mm	%
10	50	13	16.6	87
10	100	32	11.1	68
10	180	81	2.2	19
20	30	8	17.5	92
20	60	24	10	76
20	95	80	1.3	20
30	30	9	16	91
30	50	27	7.1	73
30	65	83	0.7	17

aimed at reducing groundwater recharge can be recommended with confidence.

EFFECT OF SOIL AND VEGETATION ON GROUNDWATER RECHARGE

Increased groundwater recharge following clearing and agricultural development, and the subsequent development of groundwater discharge, has created a groundwater flow system that is effectively leaching ions, once stored throughout the regolith, toward the discharge sites. Less recharge occurs under forest than under cleared land since the frequency of soil saturation and deep percolation there is much less. For example a paired catchment study of forest and cleared land near Bendigo (Dyson & Jenkin 1980) showed that forest catchments maintain the soil water content at or close to wilting point for most of the year, while cleared catchments with shallow-rooted native pastures may be at field capacity for up to six months at a time. The deep-rooted forests, through evapotranspiration, maintain the ability of the soils to store soil water, consequently, these seldom saturate and drain. The cleared land with shallow-rooted pastures, however, is unable to store water through the late Autumn-early Spring period and saturation, deep percolation and groundwater recharge occur following rainfall.

The role of vegetation is also reflected in the groundwater hydrographs of the forested and cleared catchments (Fig. 1). During 1981, piezometric heads in all cleared catchments monitored rose by 0.5-0.75 m, while heads under forested catchments remained unchanged. However, the effect of forest cover does not extend into the adjacent cleared land as piezometers located at forest margins also exhibited increased heads.

The variation in piezometric surface throughout 1981-82 is an indication of the dynamic nature of this deep regional groundwater. The 1981 year was one of the highest rainfall years on record and 1982 one of the

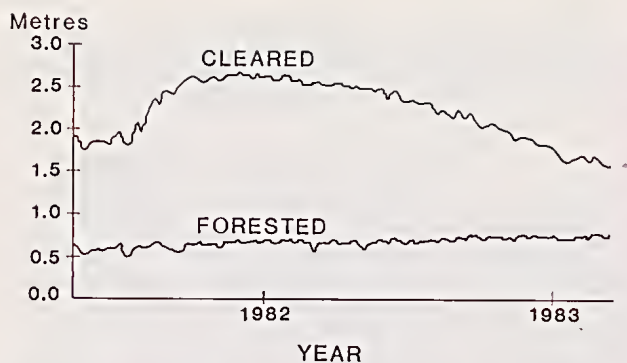


Fig. 1—Fluctuations of potentiometric levels (above 210 m datum) with time—forested and cleared catchments.

driest. Groundwaters of the cleared catchment have responded accordingly (Fig. 1). Piezometric heads rose during the very wet winter and continued to rise despite lack of rainfall until early summer when they began to decline. Heads have continued to steadily decline to the present date (March, 1983), principally because of lack of rainfall.

SUMMARY AND CONCLUSIONS

Secondary dryland salinity throughout Victoria is mostly the result of saline groundwater discharge. Changes in ecology have occurred since European settlement with the development of current agricultural practices. This has altered the magnitude of components of the hydrological cycle. The ability to store water in groundwater systems has been depleted and groundwater now discharges where previously, under natural conditions, it did not do so.

In many areas, discharge is inhibited by overlying clayey alluvium or by the heavy clay pallid zone of lateritic remnants which occur as isolated pockets throughout the Uplands, along the upland front, and extensions in the Dundas Tablelands. In these circumstances, groundwater becomes semi-confined and deep wells and piezometers are often artesian. Large areas of salt-affected land are common in such landscapes and are necessary to maintain the present approximate hydrological balance between recharge and discharge, i.e. the area of discharge sites (where groundwater moves upward through slowly permeable semi-confining layers) must be large enough to dispose of the volume of water from recharge sites.

However, where groundwater is unconfined, saline discharge occurs in the lower areas as the water table reaches the surface. This occurs in many instances throughout the Uplands where stream and river erosion has exposed the bedrock aquifer. Recharge to these aquifers is also related to low water use by vegetation, although the hydrological properties of the soils suggest that some land components may be more important than others. In particular, the shallow gradational soils and rocky ridge land component may contribute far more to recharge than the valley slopes and floors which generally carry well-developed duplex soils with medium to heavy clay subsoils.

Increased groundwater recharge following European settlement is the result of decreased water usage in the new ecology. Water passes beyond the shallow root zone of the introduced species and the soil saturates and drains to the underlying groundwater more frequently. Groundwater migrates from recharge sites to discharge sites and the activation of these flow systems is progressively leaching ions once stored in the unsaturated regolith. These ions now appear in the baseflow component of streams or concentrate by evaporation in surface soils of discharge zones, producing salt affected land.

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LAND MANAGEMENT, WATER USE AND SALINITY PREVENTION

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ABSTRACT: Agriculture in southern Australia which developed after clearing of native vegetation has allowed more water to drain through the profile leading to secondary salinity. The northern slopes region of Victoria is used as an example to illustrate the importance of the interaction between soils, climate and land use, particularly in the winter months when precipitation is usually greater than potential evaporation. The evaporation from different types of plants is discussed in relation to the hydrological significance of this excess of precipitation.

Land management to control water moving to the watertable is based on the manipulation of the species grown, particularly in relation to root growth, and some suggested strategies are given. If instead of replacing the native forest species which are deep rooting with wheat, they are replaced by agricultural species with appropriate root characteristics (e.g. lupins and lucerne) then it is suggested the water percolating to the watertable will be lessened and soil salinity reduced or prevented.

Secondary salinity in dryland areas of southern Australia has occurred following the removal of native vegetation and its replacement by agricultural species. These species transpire less water than the original vegetation resulting in greater drainage through the root zone. This drainage leads to rising levels of the water table and, in many cases, soil salting occurs as a consequence. Agricultural plants appear to have the capacity to use the volume of water escaping beyond the root zone (Peck 1977).

In the groundwater intake zone a wide range of climate, soil, geomorphology, land use, and land management occur and the quantity of water reaching the watertable is influenced by all of these factors. This paper discusses a simplistic hydrological model, the water use of native vegetation and introduced species and then deals with the potential for changing water use patterns of agriculturally important species on the duplex soils of north central Victoria, with a view to reducing through drainage.

WATER BALANCE

Where rainfall is the sole source of water, input (P) is equal to the output ($Ea + R + D$) plus storage (S), that is

$$P = Ea + R + D + S$$

P = rainfall

Ea = actual evapotranspiration

R = runoff

D = drainage

S = change in soil water content.

Applying this to the dryland farming areas of north central Victoria, manipulation of D can only be achieved by adjusting Ea . Runoff and drainage will increase as soil water content increases and there appears to be little opportunity for decreasing D by increasing R . Over a number of years S is zero.

North of the Great Divide in Victoria, potential evaporation (Eo) generally decreases from the north and

west to the east and south and corresponds to increasing rainfall so that in the south and east of Victoria, particularly along the divide, winter rainfall can be very much greater than Eo (potential evaporation) while in the north, average winter rainfall approximately equals Eo (Table 1). There is also a great deal of variation in rainfall from year to year. The difference between recorded rainfall and average potential evaporation for Rochester is shown in Table 2. For the 39 year period from 1941 to 1979, winter rainfall exceeded mean, winter, potential evaporation in 17 years and in 1973, the wettest winter for this period, rainfall exceeded potential evaporation by 115 mm. The level of groundwater rose substantially in 1973 (Trewthella & Webster 1978) in the irrigation areas to the north of Rochester, the rise being attributed to the very high rainfall in that year.

A daily water balance model (Arch *et al.* 1981) was used to simulate a fallow-wheat-pasture rotation for conditions likely to occur at Diggara (10 km from Rochester). This model predicted that for the period 1941-79, 21, 22, 19 and 10% of total drainage occurred in the years 1956, 73, 74 and 55 respectively. The actual drainage for these years may have been greater than the model predicted as in these very wet years, crops were often not sown, failed or were severely restricted by disease. The excess of rainfall over average potential evapotranspiration (Et), where Et takes fractional values of Eo (1.0, 0.75, 0.5, 0.25), in high, medium and low rainfall years is given in Table 2.

In 1981, another wet year, substantial quantities of water drained through the profile of agricultural catchments but little water drained through forested catchments (P. Dyson, pers. comm.). It appears that native vegetation is able to minimise drainage even in very wet years. Guthrie *et al.* (1978), working at Stewarts Creek in a wet area, but on a northern aspect of the Divide, give figures which indicate that Ea for an open forest of *Eucalyptus obliqua* and *E. radiata* is 800 mm per year.

TABLE 1
EXCESS OF RAINFALL OVER POTENTIAL EVAPORATION (mm) IN NORTHERN VICTORIA

E_o was measured using a Class "A" Pan at Rutherglen and Australian Standard Pan near Maryborough and Rochester

Station	Autumn	Winter	Spring	Summer
Rochester (north)	-182	7	-277	-530
Maryborough (southwest)	-162	47	-125	-466
Rutherglen (northeast)	-190	81	-112	-613

Holmes and Colville (1968), working on the Gambier Plain of South Australia showed that recharge of groundwater in the period 1960 to 1965 was 63 mm per year beneath grass whereas there was no recharge beneath a forest of *Pinus radiata*. This ranged from a low of 25 mm in 1961 to a high of 134 mm in 1964 when rainfall (June to December) was 386 and 748 mm respectively.

When native vegetation, including forest, is replaced by pastures and crops, E_a is generally reduced, leading to increases in drainage to the groundwater. However, some agricultural species have little impact on the hydrological balance. There appears to be a similarity in the growth habit and root morphology of lucerne and native heath when growing on sandy soils in the upper southeast of South Australia leading to similar water use patterns (Holmes 1960). This suggests that a knowledge of the water relationships of vegetation native to an area could provide guidance as to the most important attributes necessary for agriculturally important species to maximise evapotranspiration.

HYDROLOGICAL ASPECTS OF NATIVE VEGETATION

Although it is well known that little water escapes the root zone of the native vegetation to enter the groundwater, there appears to be little information on the mechanisms adopted by native vegetation to achieve this, although year round evapotranspiration usually occurs. Field measurements in the jarrah (*E. marginata*) forests of the Darling Range in Western Australia (Carbon *et al.* 1980) showed that these forests have a root system extending to 19 m although root systems may be deeper in other areas, to 50-60 m (as observed in the field). These workers did not present the water holding characteristics of the soil but it can be reasonably expected that the soil in the root zone can potentially store at least 2000 mm of water to 19 m, the quantity of water that would have to be added to the soil, when the soil was as dry as the lower limit to which plants might extract water, to raise its water content to a point where substantial drainage would occur. In the region of Western Australia, where this work was undertaken, annual average rainfall is less than 1200 mm or approximately one half of the potential water storage, so under this native hardwood forest, drainage is unlikely to occur.

The root depth of the forest and the water holding

capacity of the soil determine the amount of water that can be stored for plant use. The potential rate at which that water can be utilised is determined by the atmospheric demand (E_o) and the water content of the soil. The actual rate is largely controlled by the hydraulic conductivity and water potential of the soil, the density of roots and plant factors including susceptibility to wilt.

A greater density of roots is required for a plant to be able to meet demand on a day of high evaporation than on a day of low evaporation. Similarly a greater density of roots is required as the soil water content decreases to meet this evaporation demand. In the jarrah forest, reported by Carbon *et al.* (1980) there were sufficient roots to supply water at a rate equivalent to the highest daily evaporative demand likely in summer even when the soil water content approached the lower limit that the trees could extract.

During a 14 month period the evapotranspiration from a single pine tree (introduced species) and associated pasture accounted for all rainfall at a location in a medium rainfall region (900 mm) east of Perth (Greenwood *et al.* 1981). No water drained beyond the root zone, confirming the earlier work of Holmes and Colville (1968). Two-thirds of the yearly evapotranspiration occurred between July and December and one-third between January and June. The pine tree transpired (E_a) at a rate equivalent to evaporative demand (E_o) when adequate water was present and the ratio of E_a to E_o decreased as soil water content decreased. This is similar to the performance of other perennials (Willatt 1971) and annuals (Anderson 1980). There appeared to be no mechanism in the pine tree to delay water use or conserve water.

Native forests appear to have evolved mechanisms that also allow high rates of transpiration even when the leaves are severely stressed (Sinclair 1980, Ladiges 1974) and yet these plants recover easily when water stress is relieved (Ladiges 1974). The extensive root systems of native forests create a large volume for storage of water and allow extraction of this water to occur rapidly even under conditions that would stress agricultural species (Sinclair 1980). In dry environments, where annual potential evaporation is very much greater than annual rainfall and where annual rainfall may vary a great deal, it is this ability of native vegetation to create an extensive water storage zone rather than the perennial nature of their growth that allows the forest to minimise or prevent drainage.

TABLE 2
EXCESS OF WINTER RAINFALL OVER POTENTIAL EVAPOTRANSPIRATION
Ranking Et at 4 levels for the years 1941-1979 at Rochester, where $E_o = 125$ mm

Rank		Rain (mm)	Et = E_o	Rain - Et(mm)		
				Et = 0.75 E_o	Et = 0.5 E_o	Et = 0.25 E_o
1	Wettest winter 1973	240	115	146	177	209
10		153	28	59	91	122
20		121	-5	27	60	89
30		92	-34	-2	29	61
39	Driest winter 1944	29	-96	-64	-34	-2

Rainfall data supplied by Bureau of Meteorology.

Evaporation data supplied Tatura Irrigation Research Institute
(average evaporation 1941-1978)

THE POTENTIAL FOR INCREASING WATER USE OF AGRICULTURAL SPECIES BY MANIPULATING ROOT SYSTEMS

There is considerable evidence that root morphology and physiology influence water use of agricultural species and that there are opportunities to modify the root characteristics by both changing plants and altering management.

In the cereal belt of Western Australia, Sedgley *et al.* (1981) found nearly twice as much water drained from a subterranean clover pasture (*Trifolium subterraneum*) than from a wheat crop and attributed the difference to greater rooting depth of wheat. Nulsen and Baxter (1982), working in the same region, measured E_a from a number of crops including barley, lupins and subterranean clover and found that E_a was greatest from barley and lupins. These crops have greater rooting depth than subterranean clover (R. A. Nulsen, pers. comm.). In the New England region of New South Wales, Begg (1959) found that *Phalaris aquatica* extracted more water from the soil than native grasses and dried the soil to a greater depth, a consequence of deeper roots.

Changes in soil management have been shown to influence root characteristics of wheat. Ellington (1982) at Rutherglen in northeast Victoria has shown that deep ripping increased the quantity of roots in the 0.40-0.70 m zone from 0.06 t ha⁻¹ to 0.45 t ha⁻¹.

Late seeding, high rates of seed and high fertilizer application rates led to increased E_a by wheat at Wagga Wagga in southern New South Wales (Fischer & Kohn 1966a). Some of the increase was attributed to increased root density. Grain yield was shown to depend on the severity and timing of plant water stress and maximum yields did not necessarily correspond to maximum E_a (Fischer & Kohn 1966b). Greacen and Hignett (1976) report that low density of wheat roots restricted water use for wheat in South Australia, and yields suffered as a consequence.

There is a suggestion that root development can be manipulated by soil amelioration with gypsum in the wheat growing areas of Victoria. Experimental evidence for soils treated with gypsum shows that there is greater water use (Cooke & Willatt 1981), greater water use

efficiency (unpublished data) and greater yields (Sims & Rooney 1965, Cooke & Willatt 1981) in such cases.

GROWTH PATTERNS

Lengthening the growing season has been suggested as one means of increasing water use by plants (Malcolm 1982) but there is little evidence to support this claim and there appears to be little scope to achieve this with annuals in Victoria. For example, the seeding date for wheat is largely controlled by the selection of the optimal date of flowering which depends on incidence of frost and factors relevant to water supply (Fischer 1979). When wheat is seeded early the date of flowering is brought forward to a period where the chance of frost is high. If wheat is forced to flower later to extend the growing season, the chance of the crop maturing during a dry period is increased. Dry soil conditions during autumn prevent the use of those cereal varieties suitable for early seeding and also prevent the adoption of management practices that allow early seeding. Further, the choice of seeding date is largely controlled by climatic conditions because seeding can be delayed due to the soil being too dry or too wet. Similarly the choice of subterranean clover varieties is largely based on the chance of seed set occurring prior to water stress in late spring (Wolfe & Southwood 1980). Species which mature later, may produce more dry matter in most years but in years when water stress occurs in early spring they fail to produce sufficient seed to guarantee their persistence.

THE POTENTIAL OF ALTERNATE CROPS AND PASTURES IN SALINITY PREVENTION

One species that has considerable potential as an alternative is lucerne, of which the cultivar 'Hunter River' has been traditionally grown. This is a spring and summer growing cultivar and low winter temperatures limit its growth in northern Victoria, even though water is used during that period. In an experiment in the Northern Irrigation Region (Steed, pers. comm.) it was found that lucerne used water at a rate at least equal to E_o during the winter period when not irrigated so that although growth was slow, the crop had the potential to

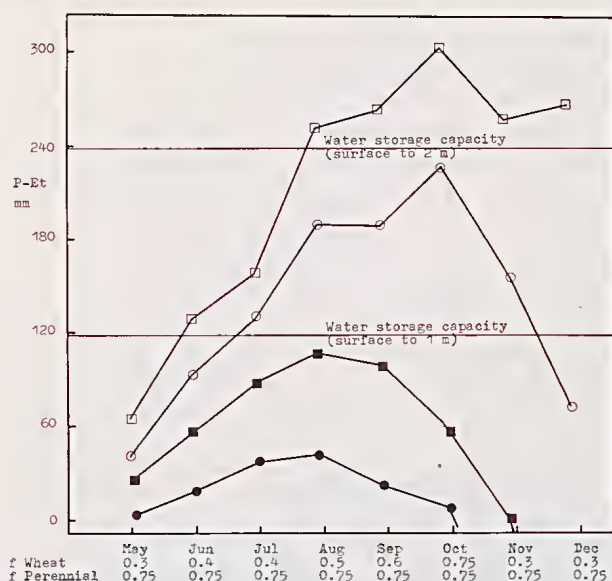


Fig. 1—Cumulative difference between rainfall (P) and potential evaporation (Et) during the growing season for an average year (closed symbols) and 1973 (open symbols) for a perennial pasture (● ○) and wheat (■ □). $Et = f \cdot E_o$ where E_o is long term average pan evaporation, Tatura, and f is the ratio of Et to E_o which is presented at the base of figure. Also shown is the storage capacity ('Field capacity' less 'wilting point') for a typical duplex soil (0.12 mm/mm).

grow rapidly when air temperatures were more favourable. In this period roots extended to 1.5 m, which is one of the necessary requirements for improved water use. When temperatures increase in spring the lucerne will grow and produce harvestable yield and use water from the entire root zone. This zone is then available for water storage when the lucerne is removed or during a wet winter even if the lucerne has not been harvested. If 1.5 m of the profile is available for storage (Cooke & Willatt 1981) then the soil can accept some 150 mm of rainfall which is adequate for the high drainage component that occurs in very wet years.

Water use efficiency, the quantity of dry matter produced for each mm of water, of lucerne is greater in spring than summer in non-irrigated areas, when values of $Ea = 0.5 E_o$ and $0.2 E_o$ respectively (Snaydon 1972). Fischer (1979) reports similar values for wheat. Thus more efficient production occurs when lucerne uses water in spring than if water use is delayed to summer. This is an important concept because annuals, which use most water in the spring when water supply can be $0.3-0.5 E_o$, may be more efficient than perennials which use water in summer when rainfall can be as low as $0.2 E_o$ or in the winter when temperature reduces water use efficiency.

It appears that there is potential for mixing pasture species (Wolfe & Southwood 1980) to optimise growth. Lucerne, Hunter River var., (winter dormant) and annual subterranean clover (winter active) can be combined so that pasture can actively grow in any season

when water is available. The winter limitation to growth in most years is low temperature, which limits water use efficiency. Fig. 1 shows the accumulation of water in the soil, estimated from the difference between rainfall and Et , under average conditions and wet conditions (1973) for a wheat crop and a perennial pasture. This illustrates that a perennial pasture with higher Et accumulates less soil water and has a greater potential to store water. Another crop strategy would be to use lupins in the drier northern regions but, as early growth of lupins in Victoria is governed more by temperature than by water supply, they may not be suitable. If water is not available in late autumn (April-May), when temperatures are satisfactory, germination will not take place; when the soil is wet in June or July (early winter) temperatures are too cool for lupin growth (Willatt & Lindsay (in prep.).

PRACTICAL IMPLICATIONS

It is likely that changes in farm management which increase evapotranspiration would lead to substantial reduction of recharge to groundwater in northern Victoria. These changes would be to provide conditions for improved root development and function, and to introduce species with improved root characteristics. In some cases, however, increased evapotranspiration could be accompanied by reduced water use efficiency.

The use of lucerne with other plants or as a rotational component appears to have potential by providing a satisfactory pasture as well as utilising large quantities of water. The selection of the most suitable species, variety and management options will be largely influenced by soil and climatic factors and be controlled by economic considerations. There will be little progress towards the prevention of dryland salinity until detailed experimentation of water use is undertaken. This work must be undertaken in the field in areas representative of known groundwater intake areas.

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THE ROLE OF TREES IN DRYLAND SALINITY CONTROL

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ABSTRACT: Tree planting is likely to play a part in control strategies for dryland salting, due to the high annual water use of trees relative to agricultural crops or pasture. Applications of tree planting include both recharge control and discharge control of salting. Efficient design of planting plans for recharge control requires identification of the areas in each catchment where groundwater recharge is most intense. Tree planting should be considered as the primary control measure in these areas, and should also be integrated with modified farming practices to minimise groundwater recharge over the remainder of the catchment. The location and density of planting needed for effective control of recharge will usually allow continued agricultural production within the planted area.

Establishment of trees within groundwater discharge areas is more difficult and is unlikely to achieve long term salinity control unless recharge control is simultaneously applied, when discharge control will hasten the reclamation of salted land. The location and density of planting required depend on the characteristics of the discharge area, and further research would be necessary to gain a full understanding of the application of tree planting in these areas.

Species selected for salinity control planting must be able to make good growth on the site to be planted, to transpire large quantities of water, and to provide other products or benefits as far as possible. Choice of species should be made on the basis of experience and local knowledge, supplemented by consideration of ecological requirements. The development of agroforestry systems which combine tree growing with conventional agricultural production without economic disbenefit will assist in the necessary introduction of large numbers of trees into farming areas.

Tree planting has repeatedly been suggested as a means of controlling salinity in Victoria and elsewhere (Morris *et al.* 1981, Greenwood 1978, Garland & Duff 1981, Anderson 1982). Although some of the suggested applications of trees are unlikely to be feasible for either physical or economic reasons, it is now apparent that successful control strategies for dryland salting will probably include tree planting in combination with agricultural and engineering measures. The purpose of this paper is to examine what part trees might play in such a combined strategy.

The potential of some tree species to control salting lies in their ability to use more water than crops or pastures on an annual basis, and to draw it from deeper in the soil profile. The primary features contributing to this effect are an evergreen perennial habit and an extensive root system; other features of importance in some species include leaf area, canopy structure and physiological factors such as the ability to continue transpiring at relatively low soil water potential. Some indigenous eucalypts are particularly well suited for salinity control planting, in addition to being naturally adapted to the Victorian climate. Some measured rates of transpiration for eucalypts and other species are listed in Table 1. An aspect of canopy structure worthy of special mention is the capacity of tree crowns to intercept incident rainfall. This may rival transpirational water use as a means by which trees limit the amount of water percolating into the soil, particularly in areas or at times of the year when rain falls predominantly as light showers. In addition to their water use, the possibility of salt uptake by trees has been considered by some as a means of lowering soil salt concentrations. The rapid growth, large stem volume and ability of some species to

resprout from a cut stump have led to suggestions of a system of short-rotation coppiced eucalypts, with salt-laden stems and foliage being harvested and removed from the site every few years. Appealing as such a scheme may be, the calculations in Example 1 show that it is clearly not feasible.

There are two distinct approaches to tree planting for salinity control. The first and most important is planting in groundwater recharge areas to reduce the volume of water passing beyond the root zone to replenish groundwater reserves; the second approach is to establish trees in discharge areas with the intention of lowering raised water tables by drawing on the groundwater for transpiration. The remainder of this paper is concerned with the question of where, how much and what species to plant for effective salinity control by each of these approaches.

RECHARGE CONTROL

Some groundwater recharge is likely to occur over virtually the whole area of most Victorian catchments, at least in wet years (Dyson & Jenkin 1981). However, the volume of recharge per unit area may vary greatly in both time and space. The amount of rainfall and evaporation, land use or vegetation type, topography, soil, and geology of a catchment all influence the quantity of water which enters the soil at a given point and passes through the profile to join the groundwater. Naturally, the larger the catchment under consideration, the more variation will be displayed in each of these factors and the more variation can be expected in groundwater recharge. Even in small catchments however it should be possible to define zones of greater and lesser

TABLE 1
SOME ESTIMATES OF DAILY AND LONGER TERM WATER USE BY
EUCALYPTS AND OTHER SPECIES

Species	Water Use	Notes
<i>Eucalyptus occidentalis</i>	558 mm over 5 months of summer	12 year old plan-plantation. (Stibbe 1975)
<i>Eucalyptus</i> species	Up to 3 mm day ⁻¹ during summer	2 years post germination. (Greenwood & Beresford 1979)
<i>Eucalyptus camaldulensis</i>	562 mm year ⁻¹	(Karschon & Deth 1967)
Mature eucalypt forest	Up to 739 mm over 16 months	(Carbon <i>et al.</i> 1982)
<i>Eucalyptus wandoo</i>	1100 mm year ⁻¹	Based on projected canopy area of scattered trees (Greenwood <i>et al.</i> 1981)
<i>Pinus pinaster</i>	Up to 738 mm over 16 months	(Carbon <i>et al.</i> 1982)
<i>Pinus pinaster</i>	Up to 610 mm year ⁻¹	(Butcher 1977)
<i>Pinus radiata</i>	910 mm over 14 months (up to 3.3 mm day ⁻¹)	(Greenwood <i>et al.</i> 1981)
<i>Pinus radiata</i>	726 mm year ⁻¹	(Holmes & Colville 1970b)
<i>Atriplex vesicaria</i>	Up to 1.3 mm day ⁻¹ during summer	(Greenwood & Beresford 1980)
Pasture	588 mm year ⁻¹	(Holmes & Colville 1970a)
Pasture	540 mm year ⁻¹ (up to 4.1 mm day ⁻¹)	Greenwood <i>et al.</i> 1982)
Maize	Up to 6.5 mm day ⁻¹	(Slabbers 1980; quoting other workers)
Alfalfa	Up to 8.5 mm day ⁻¹	

recharge potential on the basis of slope and aspect. The importance of identifying areas of high groundwater recharge lies in the possibility of concentrating salinity control efforts in these areas. Methods are available for mapping recharge contours over large areas, based on indices such as soil moisture at depth, soluble ion content, earth resistivity or other measures of the degree of leaching. Such surveys are however expensive and at best it will be some years before extensive recharge data are available for the major salt-affected catchments of this state.

Rather than delay urgently-needed recharge control measures, it should be possible to identify major recharge areas where they exist by stratification of catchments on the basis of rainfall, vegetation, slope, aspect,

and soil type, combined with existing knowledge of groundwater resources. Even a rough subjective classification along these lines should be adequate to point to the parts of a catchment where the hazard of recharge is greatest, thus allowing concentrated salinity control efforts to begin. The effects of non-uniform recharge on salinity control strategies are illustrated by the calculations in Example 2.

The distribution of groundwater recharge within a catchment may also vary from year to year. In some areas of low to moderate winter rainfall downward movement of water through the soil profile is limited by an impeding B horizon of low hydraulic conductivity. Groundwater recharge is therefore restricted, and in dry years could be confined to limited areas of shallow or coarse textured soils or bare fallowed ground. More commonly an impeding B horizon will tend to keep recharge uniform from year to year, as long as rainfall is sufficient to maintain the A horizon above field capacity through the winter. Rainfall in excess of the maximum drainage rate permitted by the impeding layer will then tend to be lost as surface runoff. This restriction of recharge is fortunate from a salinity control viewpoint, since extreme variation of recharge with time presents a problem for the design of control measures. For example, suppose it has been determined that salting in a given catchment is the result of an average increase in recharge of 20 mm per year since clearing of native forest. Strategies designed to reduce recharge by this amount may be ineffective if nine years of below average rainfall with zero excess recharge are followed by a tenth in which excess recharge is 200 mm.

The implications of recharge variability for land management in catchments subject to salting are clear. In the major or perennial recharge areas tree planting to maximise interception of rainfall and transpiration of soil water is an appropriate treatment: in many cases this will not conflict seriously with agricultural landuse since the recharge areas will tend to be on the shallow stony soils of hilltops and ridges (Jenkin 1981). In addition, agricultural practices in the rest of the catchment must be refined to allow more careful management of soil water storage. The aim should be to minimise the penetration of water beyond the maximum rooting depth of the crops or pastures grown; breeding of deeper rooted varieties of important species will help in the longer term. Thirdly, trees should be established as shelter belts, woodlots or ornamental plantings within the agricultural area, taking advantage of roadside verges and other unused land to remove some of the water stored at depth in the soil profile. By these measures the annual accession of water to the groundwater through major recharge areas will be halted or substantially reduced, and the extent of saturation of soils in the rest of the catchment minimised to provide reserve capacity for storage of water in periods of high rainfall.

Tree planting for regional recharge control is therefore of two types: 'primary' planting in the perennial recharge areas, and 'secondary' planting (combined

with modified farming practices) throughout the cleared part of the catchment. The related questions of where and how much to plant in a given situation may be considered in terms of this classification. In general, the aim must be to plant where recharge takes place and to establish a large enough area of trees at sufficient density to eliminate this recharge.

The location and extent of primary planting are determined wholly by the size and location of identified perennial recharge areas: for effective control, trees must be planted within these areas and planting must extend over the whole area. The density of planting remains to be determined, and is of considerable importance as it affects the feasibility of combining tree establishment for recharge control with grazing, cropping or other landuse within recharge areas. To obtain the maximum benefit from interception of rainfall, trees must be planted closely enough to achieve more or less continuous crown cover over the whole recharge area. While this might be necessary in some limited areas of very high recharge, it is likely that the water-using capacity of tree species chosen for recharge control will usually be great enough to utilise all the infiltrating water in transpiration; interception is then a non-essential benefit of tree establishment, and tree spacing may be increased as long as continuous root cover over the whole recharge area is achieved.

It is important to appreciate that the planting density in recharge control areas need not be as high as that of the native forests which grew there before clearing. In the natural situation, the water use of individual trees is limited by water availability in the presence of competition from adjacent trees (Figure 1). As a result, total water use per unit area may be expected to be independent of tree density over a wide range. Furthermore, the use of selected high water-using species or varieties, and the application of management practices such as thinning and coppicing should allow an increase in the annual potential transpiration rate over that of the native forest. In any case, the aim of eliminating groundwater recharge within identified perennial recharge areas is an ideal which need not be wholly achieved: a complete return to pristine conditions of groundwater recharge, watertable level or stream salinity in farmed catchments is not necessary to overcome dryland salting and restore stream water qualities to an acceptable standard. The relation between potential tree water use and the proportion of a catchment retained under forest is examined further in Example 3.

The location and extent of secondary planting for reduction of ephemeral recharge over large cleared areas are strongly influenced by the availability of land and the willingness of landholders to establish trees as shelter belts, woodlots, ornamentals or for other purposes within prime agricultural areas. Tree establishment should be concentrated in those parts of a catchment where the risk of a substantial 'overflow' of soil water into the groundwater is greatest. The characteristics of such high-risk areas are similar to those of perennial recharge areas, including high effective rainfall, rela-



Fig. 1—Expected form of the relationship between tree density and water use per unit area for high (solid line) and low (broken line) levels of potential transpiration.

tively coarse textured soils, low slopes and shallow groundwater.

The density of this type of tree establishment will rarely be sufficient to remove all the water stored or penetrating below pasture and crop root zones. The aim should be to plant as many trees as possible, without reducing agricultural productivity. There are undoubtedly many opportunities for tree planting within this constraint on most Victorian farms, and on public land in agricultural districts. Possibilities include roadsides, easements, reserves, land too steep, stony or boggy for economic agricultural use, and around homesteads. To these may be added deliberate commitments of farm land for tree growing for a specific purpose, including shelter belts and woodlots producing firewood, round timbers, pulpwood or sawlogs. In every case, benefits will accrue to the landholder and the local community, not only through salinity control but by providing shade, shelter, landscape amelioration and wildlife habitat in addition to harvestable tree products.

DISCHARGE CONTROL

Efforts to overcome dryland salting have in the past been directed mainly at treatment of the affected area to re-establish vegetation, limit surface evaporation and promote leaching. Although discharge control measures such as these are a natural first approach, the greater importance of recharge control is now widely recognised (Williamson 1981, Jenkin 1981). The vegetative cover established by careful treatment of a salt seep is at best a fragile pasture which can survive only slight grazing and must be managed separately from adjacent land; leaching of salt seep soils is often hindered by a tendency of the soils to disperse and prevent infiltration as soon as fresh water is applied. In any case leaching without deep drainage or recharge control is likely to add to the problem by further raising the watertable below a seep.

Where salting is the result of a high regional watertable, localised controls will not be adequate in the long term: new outbreaks may occur outside the range of the control measures. The use of trees as 'biological pumps' for discharge control may even aggravate the problem in

the longer term, by increasing the concentration of salt in the groundwater; on the other hand, pumping and drainage may lead to difficulties with the disposal of saline groundwater brought to the surface. It is apparent that control measures which do not rely on perpetual removal of groundwater from discharge areas, but rather are aimed at changing the hydrologic balance so that watertables move towards an equilibrium level well below the surface, are to be preferred.

Nevertheless, establishment of trees in discharge areas may be useful when combined with recharge control measures. The high annual water use and deep rooting habits of trees and the ability of some species to draw on the groundwater provide a means of lowering raised watertables in discharge areas more rapidly than may be possible otherwise. If recharge control is practised at the same time, it should be possible to stabilise the watertable below the root zone at a depth sufficient to eliminate surface discharge by capillary rise. Any increase in groundwater salinity which occurs in the interim period is therefore limited in significance, since it will no longer be necessary for vegetation to draw on this supply of water. The calculations of Example 4 illustrate the possible application of trees in a discharge control situation.

The combination of waterlogging and salt accumulation in the upper soil profile will rarely allow trees to establish and make good growth in the central, most severely affected part of a salt pan or seep. Planting may be recommended with confidence only where the cover of grasses and herbs is greater than 75%, the remainder being bare or inhabited by halophytic shrub species. Tree planting for discharge control will thus tend to surround the obviously salinised area; within the salinised area, salt tolerant grasses or shrubs could be established to reduce surface evaporation and prevent erosion. These may be replaced by a denser cover of less salt tolerant species after the watertable begins to fall and salt is leached and washed away from the surface.

Saline discharges take several different forms, and the effectiveness of control measures may vary from one to another. In particular we should distinguish the case of an unconfined or perched aquifer near the surface, from that of a deeper semi-confined aquifer discharging under pressure. A second important distinction may be made on the direction of groundwater movement to the discharge area: the case of lateral flow to the seep should be separated from that of a shallow aquifer recharged from below by upward movement of water stored in deeper strata.

For trees planted around a seep to lower the watertable, the groundwater must be accessible to their roots and of low enough salinity to be tolerated by them. Accessibility to roots requires the absence of strongly impeding horizons between the groundwater and the surface; thus it may not be possible to control discharge from a semi-confined aquifer by this approach. The maximum depth to which roots will penetrate and the maximum salinity tolerated depend on tree species and soil factors, and are at present poorly known; approxi-

mate upper limits may however be conservatively estimated as 15-20 metres depth and 8000-12 000 ppm of total dissolved salts.

Any lowering of the watertable which results from tree establishment around a seep will be a local effect, forming a groundwater depression analogous to the drawdown zone around a bore from which water is pumped. The steepness of the sides of this depression depends on the soil hydraulic conductivity; thus in heavy clay soils of low conductivity the effect of tree planting around a seep will not extend far beyond the edge of the planted strip. Under these conditions only small seeps can be wholly reclaimed by peripheral tree planting. However, over a period of 10-20 years it should be possible to reclaim larger areas by additional planting gradually advancing inwards from the original boundary of the seep.

The lateral movement of water from recharge to discharge areas requires either soils of high lateral hydraulic conductivity, or flow pathways through deep leads, shoestring sands, or fissured bedrock. Dryland salting in Victoria is typically associated with soils of low hydraulic conductivity (Dyson & Jenkin 1981); thus water movement is predominantly downwards in recharge areas and upward in discharge areas and there is little opportunity to intercept lateral groundwater flow by tree planting or other means. In situations where lateral flow pathways can be located and are accessible to tree roots, the limitations described in the previous paragraph do not apply. By establishing a sufficient number of trees in the appropriate location, the lateral flow of groundwater to the discharge area can be diverted into a transpiration flow through the trees and the salinised area reclaimed.

What constitutes 'a sufficient number of trees' for this or other discharge control planting is however difficult to determine. Even if the annual water use of individual trees can be reliably estimated, the rate of groundwater flow to the discharge area usually remains unknown. The extent to which roots intercept the lateral flow or the upward movement of groundwater, the effects of salt accumulation on tree water use and the ability of roots to draw on a semi-confined aquifer discharging under pressure are at present unknown factors, but together they determine the number of trees which must be planted for successful discharge control. A simple first approach is to measure or estimate the annual outflow of a seep and plant enough trees to use this amount of water, based on their expected individual water use under the prevailing site conditions. In fact, somewhat more than this number of trees must be planted if a lowering of the watertable is to be achieved rather than just a reduction of the outfall to zero. This approach assumes that the trees completely intercept the flow of groundwater to the seep, or draw directly on the aquifer supplying the saline water. If it is possible for tree roots to penetrate a semi-confined aquifer discharging under pressure, the effect of their water uptake on the rate of seepage will depend on the static head of water in the aquifer.

Clearly further research, in the form of both theoretical studies and empirical field trials, would be necessary to gain a full understanding of the circumstances in which discharge control by tree planting is feasible and the means of achieving it. However, it is unlikely that such detailed research into discharge control is justifiable in view of its limited application. Scarce research funds are for the time being better directed toward the evaluation of species for recharge control planting, the economics of combined agricultural and tree planting control strategies, and the location of major recharge areas.

SELECTION OF TREE SPECIES

There are three main criteria to take into account when selecting tree species for planting in catchments with salinity problems. These are:

- 1, adaptation to site—the ability to establish, grow and maintain a healthy condition over an extended period;
- 2, the capacity to transpire large quantities of water, including the ability to tap the groundwater where appropriate;
- 3, the provision of economic and other benefits in addition to the lowering of watertables and control of salinity.

ADAPTATION TO SITE

Because dryland salinity is widespread the range of environments into which trees may be planted is considerable. There is a need to identify major site types and define them in terms of environmental factors of importance to tree survival and growth. In particular, hilly or undulating country may require stratification on a local or micro-scale. A single species is unlikely to succeed, or at least be the most desirable species, over all the site types under consideration.

Although dryland salting in Victoria commonly occurs in areas of relatively low rainfall (Anon. 1982), the selection of trees for salinity control planting is by no means confined to dry country species. The perennial recharge areas in which clearing of native forest has contributed most to raised regional watertables are likely to be found in the upper reaches of major catchments, with rainfall up to 1 000 mm or more per annum. The range of sites where trees may be planted for salinity control extends from these areas of potentially high productivity to saline soils in low rainfall groundwater discharge areas where survival of the planted trees is the best that can be aimed for, and there is little prospect of economic production.

It is therefore apparent that there will be a wide range of tree species of potential use in the control of salinity. To determine the range of site conditions in which promising species make good growth, it is desirable that field trials of selected species be established on a number of sites covering the range of conditions in which salinity control planting is likely to be undertaken. Since a reliable assessment of species per-

formance may not be made for some years after planting, these trials should be commenced as soon as possible.

A rationale for the choice of species for field screening should include both theoretical and empirical approaches. The theoretical approach entails the selection of potential species from environments with similar climatic and edaphic regimes to those of the environment of introduction. Species which overlap a wide range of environment such as *Eucalyptus camaldulensis* Dehnh. (river red gum) and *Acacia melanoxylon* R. Br. (blackwood) are also obvious candidates for inclusion.

The empirical approach draws from the reservoir of local knowledge and a study of previous plantings and indigenous vegetation. A considerable body of knowledge is already held by government departments and individual landholders as to the tree species most likely to grow well under given local conditions. Indigenous vegetation merits special consideration because of its long period of adaptation to and evolution with the local environment. Remnant patches of native vegetation enable an accurate and quick assessment of the potential of indigenous species in revegetation. These species have the advantages of low maintenance and natural regeneration when re-established as viable patches of forest with component understorey species. Some degree of protection from grazing is necessary to maintain the integrity of such ecosystems. Occasionally man-induced changes will render an indigenous species unsuitable for replanting, for example *Eucalyptus macrorhyncha* F. Muell. ex Benth. (red stringybark) will not persist in grazed areas due to ringbarking by stock. On a broad scale, dieback and death of isolated eucalypts in the rural landscape, from a variety of causes, indicates the instability of such systems (Kile *et al.* 1980).

Combining the theoretical and empirical approaches may lead to a finer resolution of species choice. For example preliminary empirical investigations may indicate *Eucalyptus globulus* Labill. (southern blue gum) to be a suitable species for planting in wetter areas. A study of the natural occurrences of this species and its subspecies may then indicate the existence of populations adapted to dry, saline or waterlogged sites. Collection of seed from these populations could lead to a considerable extension of the planting range of this species. Once the potential of a species for widespread planting has been recognised, more intensive forms of selection including screening and breeding for desired characteristics may follow. Vegetative propagation (cloning) provides a suitable technique for capitalising on the gains of selection and breeding. For example, seedlings of *E. camaldulensis* have been selected for sodium chloride tolerance and vegetatively propagated to provide planting stock for saline sites (Ralph 1981).

CAPACITY TO TRANSPIRE LARGE QUANTITIES OF WATER

The major objective of planting trees in salinity-prone catchments is to lower watertables. Therefore species selected should be those which will transpire and intercept maximum quantities of water. This is true

whether the trees are planted to reduce groundwater recharge by absorbing soil water and thus preventing deep percolation, or to draw directly on the groundwater by root proliferation within the capillary fringe.

Trees have evolved in environments of differing moisture regimes and as a result individual species tend to operate at different levels of carbon assimilation and water loss. These levels have been described as ranging from adventurous (high rates of carbon assimilation and consequently transpiration; exemplified by many eucalypts) to conservative (low rates of carbon assimilation and transpiration, as displayed by *Casuarina* species) (Ashton *et al.* 1975). Greenwood and Beresford (1979) have directly measured transpiration rates in young eucalypts using a ventilated chamber technique. Their results indicate that there are significant differences in transpiration rates between different species but that the rankings change with age and vary between sites. Investigations of leaf area index in eucalypt stands in southwestern Australia suggest that five-year-old regrowth may have a leaf area index equivalent to that of mature forest (Carbon *et al.* 1979). This suggests that some eucalypt stands may reach their maximal transpiration capacities at an early stage in stand development. This fact should be taken into account when assessing the potential for replanted trees to modify the hydrological characteristics of a catchment.

For the purpose of maximizing water use it is desirable to select species which exhibit adventurous characteristics. However, it is imperative that tree species are planted only on sites which can meet their requirements. For example, seedlings of *E. globulus* planted above a saline seep in southwestern Australia grew prolifically for several years but during a dry period some saplings suffered dieback and death. Subsequently most saplings staged a recovery, but the lesson of growing species only on suitable sites remains. Research is required to elucidate a, those species which can utilize maximal quantities of water for different site types, but survive when conditions become adverse; and b, those species which predominantly use groundwater in supplying their moisture requirements. These species have the advantages of having access to a more or less permanent supply of water and importantly providing minimal competition to crop plants for top soil moisture.

It is apparent that species which grow rapidly, develop high leaf area indices and exhibit mesophytic characteristics are the prime candidates for this research.

BENEFITS OTHER THAN SALINITY CONTROL

Where several species are available which fulfil the adaptability and water use criteria, these species should be screened for their potential to supply economic and other benefits. Some products associated with tree growing which provide easily measured economic benefits include sawn timber, pulp, fuelwood, eucalyptus oil, livestock fodder and honey. Other benefits such as shade, shelter, nutrient cycling, erosion control, landscape amenity and wildlife habitat are less easily quan-

tified; these benefits will vary with location and individual farmers will attach different importance to them.

The tendency of trees to adversely affect adjacent pasture varies between species, and this may be a factor in selecting species for agroforestry enterprises (Anderson 1982).

The introduction of trees in large numbers into agricultural areas will be favoured if tree growing can be integrated with conventional farming practices without economic disadvantage. Some examples of schemes which may prove to be of benefit to landowners in the recharge zones of salt-prone catchments are a, the establishment of *Pinus radiata* D. Don (radiata pine) woodlots or incorporation of this species in an agroforestry system (Anderson & Batini 1979). The high growth rates, adaptability to a wide range of sites and forestry potential of this species should allow economic wood production as well as reduction of groundwater recharge; b, in the 400-500 mm rainfall belt an agroforestry system consisting of *E. polybractea* R. T. Baker (blue mallee) and *Medicago sativa* L. (lucerne) producing both eucalyptus oil and pasture (Anon. 1976). The ability to clone the high oil yielding varieties of *E. polybractea* would considerably enhance the economics of this system; c, fast growing eucalypts planted along drainage lines in midslope positions could yield sawn timber, farm timbers and fuelwood. In wetter zones *E. globulus* and subspecies, and *E. viminalis* Labill. (manna gum) show promise while in lower rainfall areas *E. camaldulensis* and *E. occidentalis* Endl. (yate) may be the most useful species.

In saline discharge areas where the groundwater is known to be accessible and not excessively saline, the planting of salt tolerant *E. camaldulensis*, *E. occidentalis* and possibly other species on and adjacent to salt affected land may lower local watertables, minimise soil erosion and provide forest products. The development of salt tolerant clones of eucalypts is a new and exciting prospect; however, these clones will require field testing over a period of time before their merits can be reliably assessed. If the clones prove useful then the establishment of clonal plantations will need to be based on a wide range of clones, because of the inherent dangers of establishing large areas of genetically uniform plant material.

CONCLUSION

While tree planting will only form one part of the control strategy for dryland salting in any catchment, it represents a readily available and highly flexible means of reducing the excessive intake and storage of groundwater responsible for raised watertables in many areas of Victoria. The technical difficulties of designing and implementing a large scale tree planting scheme are not great, but the economic problems are formidable, especially where planting is required on productive agricultural land. More work is needed to determine estimates of the costs of realistic salinity control

strategies in representative areas, and to explore possible funding arrangements and incentives for salinity control measures including tree planting on farms in salt-affected catchments.

Further research is also required to define the modified agricultural systems which may be employed to minimise recharge from farmland, and determine their effectiveness for this purpose. However, because of the continuing expansion of salt-affected areas and the high cost of lost production from them it is vital that detailed planning and implementation of control strategies for major catchments begin as soon as possible on the basis of existing knowledge, rather than awaiting the outcome of what may well be long term research studies.

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APPENDIX

EXAMPLE 1. POTENTIAL OF TREES FOR DESALINATION OF SALINE SOILS.

(a) Foliar salt content of eucalypt foliage under saline conditions:

Field trials have shown chloride content of several eucalypts and other native species on a highly saline site stabilises at 1-1.5% of dry weight. This corresponds to a sodium chloride content of about 1.6-2.4%, or 2% as an average figure.

(b) Biomass accumulation by planted eucalypts:

Taking fertilised *Eucalyptus grandis* W. Hill ex Maiden (flooded gum) as a source of optimistic growth estimates (Bradstock 1981)—

$$\begin{aligned}\text{Total biomass at age } 2 &= 1.8 \text{ kg m}^{-2} \\ \text{at age } 11 &= 8.4 \text{ kg m}^{-2}\end{aligned}$$

(c) Potential salt uptake:

Assuming stem salt concentration is similar to foliar concentration (approximately 2% of dry weight) the expected salt uptake by trees on a saline site is:

$$\begin{aligned} &36 \text{ g m}^{-2} \text{ after 2 years} \\ &168 \text{ g m}^{-2} \text{ after 11 years} \end{aligned}$$

(d) Salt storage in the soil:

For a moderately saline clay soil containing 0.2% salt, with bulk density of 1.2, salt content is 2.4 kg m^{-3} . Thus for a soil depth of 1 m this soil contains $2.4 \text{ kg m}^{-2} \text{ NaCl}$.

Desalination by harvesting of eucalypts would thus require about 70 two-year rotations or about 14 eleven-year rotations, assuming no more salt enters the profile in that period.

EXAMPLE 2. ESTIMATION OF RECHARGE RATES AND AREAS IN A CLOSED CATCHMENT.

Consider a catchment with a total area of 120 ha, in which groundwater discharge takes place at 100 mm per year over a 20 ha discharge area. Assume that all of this groundwater comes from uniform recharge over the remaining 100 ha; there is no groundwater flow into or out of the catchment.

$$\begin{aligned} \text{Annual discharge} &= \text{annual recharge} \\ &= 2000 \text{ ha mm or } 20 \times 10^6 \text{ litres} \end{aligned}$$

and recharge over the upper catchment area is 20 mm per annum; it should be possible to prevent this recharge simply by modifying agricultural practices, thus overcoming the discharge problem.

Now suppose recharge is not uniform: let 90% of recharge occur on a limited area of 10 ha, while the remainder is evenly distributed over the other 90 ha.

Recharge rates are now 180 mm per annum on the intense recharge area, and 2.2 mm per annum in the diffuse recharge zone. Modification of existing land use practices is unlikely to be sufficient to control recharge in the intense area, but the establishment of trees there could enable control.

Alternatively, suppose the annual rainfall in the recharge area is a uniform 400 mm. If it is suspected that an intensive recharge zone exists, its maximum area can be estimated. Assuming that say 50% of rainfall on the intense recharge zone is lost as runoff or evaporation, the actual recharge rate there is 200 mm per annum. This will provide all of the 2000 ha mm of discharge if its area is 10 ha. A rough calculation such as this may be helpful in planning the scale of tree planting needed for recharge control of salinity in a catchment.

EXAMPLE 3. RELATING RECHARGE PLANTING AREAS TO POTENTIAL FOREST WATER USE.

Consider a forested catchment of area H ha in which no recharge takes place. C ha are now cleared for agriculture, and groundwater recharge takes place over this area at R mm per year. The volume of annual recharge from the catchment is RC ha mm.

If the actual water use of the forest area is A mm per year and its potential water use given an unlimited water supply is P mm per year, then the unused transpiration capacity of the forest is $(P-A)(H-C)$ ha mm per year.

Assuming free movement of soil water from the cleared area to the root zone of the remaining trees, no groundwater recharge will occur as long as $RC \leq (P-A)(H-C)$, that is, as long as:

$$\frac{C}{H-C} \leq \frac{P-A}{R}$$

From this formula we may calculate the minimum proportion of a catchment to be retained or replanted as forest, for an expected value of potential tree water use. For example, suppose $A = 500$ mm per annum and $R = 20$ mm per annum; establishment of trees on 5% of the catchment will be sufficient to prevent groundwater recharge if P is at least 880 mm per annum. This potential water use is not unrealistic given the measured transpiration rates of well watered trees.

Tree cover of 5% is afforded by a series of three or four row windbreaks 10 m wide at intervals of 200 m across the catchment; however, the assumption of free movement of soil water to the tree root zone would not be met under these conditions.

EXAMPLE 4. MODELLING THE EFFECTS OF TREE PLANTING ON GROUNDWATER SALINITY AND DISCHARGE.

Consider a discharge area 1 ha in extent. The aquifer beneath this area contains 50 Ml of water at a salinity of 6000 ppm total dissolved salts (a 10 m aquifer thickness, assuming 50% porosity). We may study the effects of different inputs and outputs of groundwater with the aid of a simple model:

$$S_n = \frac{S_{n-1} \cdot V_{n-1} + I_n \cdot C - O_n \cdot S_{n-1}}{V_n}$$

$$V_n = V_{n-1} + I_n - O_n - T$$

where S_n = groundwater salinity in year n

V_n = volume of groundwater in aquifer in year n

I_n = groundwater inflow to discharge area in year n

O_n = groundwater outflow from aquifer in year n

C = inflow salinity (6000 ppm)

T = annual water use by trees

Four cases may be considered:

- inflow constant, 5 Ml per year at 6000 ppm. Trees in the discharge area transpire 5 Ml per year, no other discharge occurs.
- inflow as above. Trees transpire 3 Ml per year, flow beyond the discharge area and loss to deeper aquifers total 2 Ml per year.
- transpiration and outflow as in (b). Inflow is affected by recharge control in the upper catchment: volume decreases by 0.5 Ml per year while salinity remains constant at 6000 ppm.

- (d) recharge control applied as in (c). No tree planting in discharge area; to the 2 Ml of outflow is added a surface seepage flow of 3 Ml per year, decreasing by 0.5 Ml per year in line with recharge.

After 10 years, the volume and salinity of groundwater in the discharge area are:

- (a) 50 Ml at 12 000 ppm
- (b) 50 Ml at 9016 ppm
- (c) 22.5 Ml at 12 345 ppm (watertable lowered by 5.5 m)
- (d) 45 Ml at 6000 ppm (watertable lowered by 1 m)

A comparison of results (a) and (b) shows that, while discharge area tree planting increases the salinity of groundwater, the increase is slower where flow pathways exist for movement of groundwater beyond the discharge area.

Results (c) and (d) demonstrate the effectiveness of discharge area planting in conjunction with recharge control measures. The increase in groundwater salinity in case (c) may well be acceptable in view of the greatly lowered watertable. Leaching of the surface soil and establishment of useful vegetation in the former discharge area could be safely carried out; water use by the trees in this area is no longer required.



THE POTENTIAL FOR BREEDING SALT-TOLERANT PLANTS

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ABSTRACT: The potential for selecting and breeding of plants with increased tolerance to salinity appears to be good because of the existence of heritable variation for tolerance between genera and species, within species and within cultivars. Information on the genetic control of salt-tolerance would help in its selection and breeding. However, few studies have yet been conducted on the heritability and inheritance of tolerance in different plant species.

Although intraspecific variation for salt-tolerance affords the most readily accessible source of genetic variation for selecting and breeding for increased tolerance, many plant breeding techniques exist which may offer breeders with a means of producing greater variation for tolerance than might otherwise be available in a crop species, e.g., chromosomal manipulation, somatic hybridization and plant cell culture.

In conjunction with further research on the genetic control of salt-tolerance in a crop species, research on the physiological basis of tolerance, its variation with ontogeny and the influence of the environment should lead to increases in the tolerance of crop species through selection and breeding.

PLANT ADAPTATION TO HIGH LEVELS OF MINERAL ELEMENTS IN SOILS

High levels of mineral elements in the soil can often cause serious limitations to agricultural production and land development. Approaches such as fertilizer application, soil drainage and improved irrigation management have been used in attempting to overcome these limitations. Another approach is the selection and breeding of plants for greater tolerance of the mineral element and hence greater productivity in such areas.

The potential for selecting and breeding of plants for increased tolerance of high levels of mineral elements in the soil appears to be good because of the reported existence of heritable variation for such tolerance in a large number of plant species (Humphries & Bradshaw 1976, Reid 1976, Foy & Fleming 1978, Epstein 1983). For example, variation in tolerance to heavy metals has been reported between cultivars of such species as barley and wheat (Foy *et al.* 1965), rice (Howeler & Cadavid 1976), lucerne (Ouellette & Dessureaux, 1958) and soybean (Armiger *et al.* 1968) as well as between plants in ecotypes of certain grass species (Wu *et al.* 1975). Such variation has been shown to be genetically controlled, as for instance, tolerance to aluminium in barley which is conferred by a single dominant gene (Reid 1970) and in wheat by one or more major and several modifying genes (Kerridge & Kronstad 1968). Tolerance to high levels of available copper and zinc in *Agrostis tenuis* is highly heritable (McNeilly & Bradshaw 1968, Gartside & McNeilly 1974) and additive genetic variation for tolerance to high levels of copper has been shown within tolerant ecotypes of *Agrostis stolonifera* (Wu *et al.* 1975).

The occurrence of apparently wide genetic variation in plants for tolerance to high levels of elements such as aluminium and zinc in the soil is paralleled by variation between species, cultivars and individual plants for tolerance to high levels of soil salinity.

VARIATION IN SALT-TOLERANCE OF PLANTS

Considerable research effort has been directed towards identifying plant species and varieties that are tolerant of salinity. Ramage (1980) noted that over 1500 species have been used for studying plant responses to salinity and that over 50 crop species have been evaluated for varieties that exhibit salt-tolerance, including cereal, fibre, oilseed and vegetable crops, and forage grasses and legumes.

Halophytic plant species are considerably more salt-tolerant than glycophytic species (Flowers *et al.* 1977). They can survive and complete their life cycles at electrolyte concentrations up to 600 mM with an optimum concentration for growth in the region of 20 to 500 mM (Flowers *et al.* 1977) compared with glycophytes which do not show this optimum effect and may survive up to only 300 to 350 mM (Greenway & Munns 1980). Halophytes, however, are in most cases of limited value for agricultural production and for that reason, the following discussion is limited to glycophytes.

Information from many studies is available on comparative levels of tolerance between a large number of species (e.g. Maas & Hoffman 1977). Studies of intraspecific variation for salt-tolerance have revealed large differences in tolerance, such as within crested wheatgrass (Dewey 1962), tall wheatgrass (Shannon 1978), soybean (Abel & McKenzie 1964) barley (Greenway 1962) and rice (Akbar *et al.* 1972). In some studies, however, little or no intraspecific variation in tolerance has been found, as for example, beans (*Phaseolus vulgaris*) (Bernstein & Ayers 1951) and lettuce (*Lactuca sativa*) (Ayers *et al.* 1951). The absence of intraspecific variation may be a reflection of a limited number of cultivars being tested, or possibly that little variation for this character has been incorporated in the domestication and recent breeding of the species. Variation in salt-tolerance has also been found between different populations of species occurring naturally in saline and

non-saline habitats. For instance, Hannon and Bradshaw (1968) found significant variation in salt-tolerance between different ecotypes of both *Festuca rubra* and *Agrostis stolonifera*.

There may also be variation for salt-tolerance between individuals in a population of a species. This might be expected to be larger in an open-pollinated, compared with self-pollinated, species and it has been found in open-pollinated cultivars of cotton (Maliwal *et al.* 1975), sugar beet (Ulrich 1961) and lucerne (Dobrenz *et al.* 1981).

SELECTION AND BREEDING FOR SALT-TOLERANCE

HERITABILITY AND INHERITANCE OF SALT-TOLERANCE

A primary requisite in selecting and breeding for salt-tolerance is genetic variation for tolerance in the gene pool of the species for which increased tolerance is required. Interspecific, intraspecific and intracultivar variation for tolerance provides scope for selecting for its improvement. However, information on the genetic control of tolerance would help in its selection and breeding. A knowledge of the level of heritability and the inheritance of salt-tolerance in a species can help in devising a selection strategy for tolerance, such as the intensity and number of cycles of selection necessary to effect significantly increased tolerance. It could also facilitate the incorporation of tolerance in commercial cultivars from related species or lines by hybridization and selection.

If sufficient genetic variation for tolerance exists in a species and its heritability is high, then large increases in tolerance could be expected from selection. However, if the heritability is low, a high selection intensity would be needed even for small responses to selection and large responses may, therefore, be difficult to achieve. In the latter case an alternative species may be considered that has either, or both, an inherently high level of tolerance, and variation for tolerance so that increases might be expected through selection.

Knowledge of the heritability and inheritance of salt-tolerance in most agricultural plant species is generally lacking because few studies have yet been conducted in these areas. Dewey (1962), after evaluating the salt-tolerance of 60 strains of *Agropyron desertorum*, proposed a recurrent selection and breeding program for increasing its salt-tolerance. Abel and MacKenzie (1964) found variation in salt-tolerance between soybean cultivars and Abel (1969) found that tolerance in soybean was controlled by a single dominant gene. Hunt (1965) demonstrated that mature plant salt-tolerance in *Agropyron intermedium* was heritable with a parent-progeny correlation coefficient (r) of 0.83 and a coefficient of determination, r^2 , of 68 per cent. The F_1 hybrids of salt-tolerant and -sensitive rice cultivars were more tolerant than parental lines (Akbar & Yabuno 1977) while the F_2 exhibited a wider range of variation than the parents, and tolerant progenies were selected from F_3 and F_4 generations (Akbar *et al.* 1977, Akbar & Yabuno 1977). Two types of sterility were induced by

salinity in rice and resistance to a delayed-type panicle sterility was dominant and controlled by a small number of genes (Akbar & Yabuno 1977). Norlyn (1980) found the ability of barley to yield under salinity was heritable and that its genetic control was complex. Dobrenz *et al.* (1981) utilised variation within a lucerne cultivar and obtained increased salt-tolerance during germination from selection.

SOURCES OF SALT-TOLERANCE BEYOND INTRASPECIFIC VARIATION

Although significant levels of intraspecific variation for salt-tolerance afford the most readily accessible sources of genetic variation for selecting and breeding for increased tolerance, some agricultural species either possess very little variation for tolerance or relatively low levels compared with other species. For such species consideration should be given to other ways in which higher levels of tolerance might be obtained. A number of these possible methods are outlined below. However, the success from using the following approaches depends largely on the possibility that salt-tolerance in plants is under particulate gene control.

Exploitation of alien variation for tolerance

Those salt-tolerant species and genera related to a crop plant which exhibit high levels of chromosome pairing with it could contribute useful sources of tolerance to the crop species through interspecific and intergeneric hybridization. It is possible that within the gene pool of an agricultural species, amongst its "wild" and "weed" related species, significant amounts of variation for this character may exist. For instance, little variation for tolerance was found in the commercial tomato *Lycopersicon esculentum*, but crosses with the salt-tolerant related species *L. cheesmanii*, followed by several backcrosses to *L. esculentum*, gave plants with higher levels of tolerance than the commercial tomato, although with reduced fruit size (Rush & Epstein 1976).

In many interspecific crosses, fertilisation and early embryo development occurs but embryo death may result from malnutrition due to endosperm failure (Raghaven 1977). Embryo culture, involving the excision of such embryos and their culture on nutrient media, has been used successfully for interspecific hybrids in cotton, barley, tomato and rice, and with intergeneric hybrids of *Hordeum* and *Secale*, *Triticum* and *Secale*, and *Tripsacum* and *Zea* (Yeung *et al.* 1981). The technique may, therefore, broaden the range of cross compatibility between crop plants and their related species and genera for breeding for salt-tolerance by providing access to a greater range of variation for this character.

Chromosome manipulation techniques, such as chromosome addition, substitution and translocation provide the potential to transfer salt-tolerance into the genome of a crop plant from species and genera related to the crop species, but whose chromosomes do not pair, or show only little pairing with those of the crop plant. The successful use of these techniques in plant breeding, as for instance the transfer of stem, leaf and

stripe rust resistance from *Agropyron intermedium* into wheat by chromosome addition, substitution and translocation (Wienhues 1966) indicate the feasibility for their successful use in incorporating salt-tolerance in crop plants. One possibility for the application of these techniques is the transfer of the high level of salt-tolerance of *A. elongatum* into wheat. Success from the use of such techniques will depend in part on the expression of salt-tolerance of the related species being maintained in the genetic background of the crop plant, and on the absence of deleterious effects of the substituted or added chromosome or translocated segment bearing salt-tolerance on the adaptability and yield of the crop plant.

Somatic hybridization, resulting from the fusion of protoplasts derived from different species, also offers the potential for transferring genetic information for salt-tolerance from one species to another. Smith *et al.* (1976) recovered mature hybrid plants between two species of tobacco, *Nicotiana glauca* and *N. langsdorfii*, by protoplast fusion. However, there are few other reports where this technique has resulted in hybrids.

Other techniques useful for interspecific hybridization are discussed by Stalker (1980), some of which may be useful for transferring salt-tolerance to an agricultural species from other species within its gene pool.

Induction of variation for salt-tolerance

The induction of variation in salt-tolerance by mutagenic agents such as chemical or radiation treatments, offers the potential for providing new sources of variation for this character. Induced mutation techniques enable the full range of naturally occurring mutations to be produced plus those that have been lost through natural selection, and possibly new forms of mutant expression. These techniques have been used to produce new sources of genetic variation for characters such as yield, and pest and disease resistance in a number of agricultural species (Anon 1970). For example, Gustafsson (1941) induced cold resistant barley mutants by irradiating seeds with x-rays.

Plant cell cultures, which can be derived from virtually any part of a plant, including root or stem sections, cotyledons and leaves (Scowcroft 1977), afford the opportunity of screening large numbers of cells for salt-tolerance. Dix and Street (1975) used callus cultures derived from petioles of *Nicotiana sylvestris* and *Capsicum annuum* to select cell lines capable of growing in liquid media containing one and two per cent (w/v) NaCl. Similarly, Nabors *et al.* (1975) selected cell lines derived from stem sections of *Nicotiana tabacum* which were tolerant of a growth medium containing 1.6 g/l NaCl and Croughan *et al.* (1978) selected a cell line derived from lucerne cotyledon tissue with increased growth under a range of NaCl levels compared with an unselected cell line. To date there is no evidence to judge whether plants regenerated from such tolerant cells are also tolerant to high NaCl concentrations. Success with this technique will depend on whether cell and whole-

plant tolerance to NaCl are closely associated. Recent studies by Tal *et al.* (1978), Orton (1980) and Smith and McComb (1981 a, b) found that the growth responses to NaCl of whole plants and callus (from hypocotyl tissue) were very similar for tomatoes, barley, lucerne, white clover, strawberry clover, beans, and sugarbeet.

A further potential benefit of plant cell culture techniques in searching for salt-tolerance is the occurrence of large amounts of genetic variation in plants regenerated from cell cultures which could possibly embrace variation for increased tolerance. For instance, Shepard *et al.* (1980) found significant variation for tuber size, maturity date, photoperiod requirement and resistance to late blight (*Phytophthora infestans*) in somaclonal lines derived from leaf protoplasts in potato. Somaclonal variation has also been demonstrated for rice (Nishi *et al.* 1968), sugarcane (Heinze & Mee 1969), and oats (Cummings *et al.* 1976). Consequently, this technique appears to offer breeders with a means of producing greater variation for tolerance than might otherwise be available in a crop species.

FACTORS INFLUENCING THE SELECTION AND BREEDING FOR SALT-TOLERANCE

While a primary requirement in selecting and breeding for increased salt-tolerance is the existence of heritable variation for it, there are several factors which can influence the level of tolerance in a plant population, which are as follows:

Indices of salt-tolerance

A range of criteria, or indices, have been used in evaluating salt-tolerance in agricultural plants, including percentage germination, shoot dry weight, shoot number, leaf necrosis and seed yield. Different plant characters can exhibit differing responses to salinity, for example Ayers *et al.* (1952) found seed production in barley and wheat was decreased less by salinity than was vegetative growth measured as shoot dry weight. Consequently, the level of salt-tolerance between and within species is likely to vary according to the criteria used to evaluate its effects on growth and productivity.

Stage of growth and tolerance

The influence of salinity on plant growth has been studied as its effects on germination, seedling emergence, seedling and later plant growth, flowering, seed set and vegetative regrowth (of perennials). Salt-tolerance in a plant species appears to vary during its ontogeny. For instance, wheat and barley are more sensitive to salinity during early seedling growth than at germination or during later growth (Ayers *et al.* (1952) while sugar beet is more sensitive to salinity during germination than during other growth stages (Bernstein & Hayward 1958). Because of these differences, some studies have been concerned with selecting for salt-tolerance under saline conditions imposed over the entire growth cycle, as with tomato and barley (Epstein *et al.* 1980). However, if a constant salt concentration is used in such an approach, because of the possible variation in tolerance at different growth stages the selection

intensity for tolerance will in consequence vary with stage of growth. Varying the concentration of salt during selection according to the sensitivity of the stage of growth may be a practical alternative. A further option would be to screen separately for tolerance at each stage of growth, allowing a salt concentration during each stage to provide the appropriate selection intensity and permitting additional cycles of selection on those growth stages with relatively low heritabilities for tolerance. Lines selected for tolerance at particular stages of growth could be recombined and their segregates screened for overall tolerance throughout plant growth.

In some species selection for increased salt-tolerance may be necessary at only one growth stage. For instance, sugar beet is highly sensitive to salinity only at germination (Bernstein & Hayward 1958) and selection for tolerance during this stage should remove a limiting step to tolerance throughout its growth.

Knowledge of the physiological basis of salt-tolerance

Reviews by Greenway and Munns (1980), Hsiao (1973), Jennings (1976) and Maas and Nieman (1978) provide an excellent coverage of current knowledge of the physiological basis of the response of plants to salinity. However, limited information is available on the comparative physiology of genetically closely related plants that differ markedly for salt-tolerance. Comparisons have been made between species of a different genus for differences in characters such as ion uptake, organic solute concentrations and ion distribution when grown under high levels of salinity. However, as indicated by Epstein (1980), these differences are to be expected simply on the basis of phylogenetic differences between them. As an alternative, Epstein (1980) proposed that if plant breeders can identify closely related genotypes that differ markedly in salt-tolerance, such as species of one genus or genotypes within a species or cultivar, then such populations would be useful in determining the physiological basis of salt-tolerance in a species. Such studies could provide breeders with physiological or morphological criteria for selecting for increased tolerance. Criteria based on mechanisms that confer tolerance are more likely to be more accurate indices of tolerance than those based on a phenotypic character, such as yield, which are strongly influenced by the environment and can also give inflated estimates of tolerance due to hybrid vigour.

Examples of comparative studies between related genotypes differing in salt-tolerance include that of Abel and MacKenzie (1964) who found differences in tolerance between salt-tolerant and -sensitive soybean cultivars was associated with differences in their ability to exclude chloride ions from the stems and leaves. Rush and Epstein (1976, 1981) found the higher salt-tolerance of the "wild" tomato, *Lycopersicon cheesmanii* ssp *minor*, compared with the commercial *L. esculentum*, was associated with lower levels of total amino nitrogen, specific amino acids and free acidity, and higher shoot concentrations of sodium, while Tal *et al.* (1979) found

the tolerant "wild" tomato *L. peruvianum* had half the proline but double the chloride concentration of *L. esculentum*. Hannon and Barber (1972) investigated physiological differences between ecotypes of *Festuca rubra* which Hannon and Bradshaw (1968) had found to differ for salt-tolerance. Tolerance was found to be associated with a greater ability to exclude sodium and chloride ions from the shoots.

Influence of environment

Comparative studies of the salt-tolerance of plants have been conducted under a range of environmental conditions, including different temperatures, humidities, daylengths and light intensities, with plants grown in different growth media, such as water culture and artificially salinized soils. Similarly, a range of salts (e.g. NaCl, Na₂SO₄, KCl, NaHCO₃, MgCl₂ and CaCl₂) have been used to study the influence of salinization on plant growth. Variation in these factors has been shown to influence the level of salt-tolerance in plants (Bernstein & Hayward 1958, Nieman & Poulsen 1971, Bernstein & Francois 1973, Bernstein *et al.* 1974, Nieman & Shannon, 1977, Maas & Hoffman, 1977). Differences in environmental conditions, both root and aerial, between different studies makes it difficult to make close comparisons between their results. For example, many crops seem less tolerant of salinity when grown under hot dry compared with cool humid conditions, although all crops are not equally affected (Maas & Hoffman, 1977). Consequently, environmental factors must be considered when evaluating and selecting for salt-tolerance.

One environmental factor that appears to influence the effect of salinity on plant growth and which is worthy of consideration, particularly in Australia, is low root-zone oxygen concentration. Waterlogging of the soil and salinity can occur together in both irrigated conditions where there are poorly drained soils, and under dryland conditions in saline seeps. Studies of soil-oxygen deficiency and high soil salinity in citrus (Pearson *et al.* 1957), tomatoes (Aubertin *et al.* 1968, West & Taylor 1980b), oats (Abd-El-Kadous 1974), apple trees (West 1978) and beans (West & Taylor 1980a) indicated the compounding effect of soil-oxygen deficiency on that of salinity on plant growth. West and Taylor (1980a) noted "while some agronomically important plants may be reasonably well adapted to either salinity or to oxygen deficiency (waterlogging), there is no information which suggests that these plants are adapted to both conditions together".

FUTURE PROSPECTS FOR SELECTING AND BREEDING FOR INCREASED SALT-TOLERANCE IN AGRICULTURAL PLANTS

Genetic variation for salt-tolerance in many agricultural plants appears to be available from a range of different sources. Further research on new plant breeding techniques should further expand the range of available genetic variation for tolerance. Knowledge gained from further research on the physiological basis of tolerance and its variation with ontogeny should permit the refinement of selection and breeding techniques.

It does not appear feasible to breed glycophytic

plants with levels of salt-tolerance as high as those of halophytic plants because of basic physiological differences in their response to salinity. Halophytes have the ability to accumulate ions such as sodium and chloride to high internal concentrations while glycophytes respond to salinity basically by ion exclusion (Flowers *et al.* 1977, Greenway & Munns 1980). In breeding glycophytes for salt-tolerance, however, it may be possible to effect, for example, substantial increases in the threshold level of salinity at which significant yield reductions take place or to reduce the yield decline per increment in soil salinity within the range where yield is adversely affected. Such changes would not require a major alteration to an existing physiological mechanism(s) of tolerance, but rather a selection for maximum efficiency of this mechanism(s).

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ECONOMIC ASPECTS OF THE CONTROL OF DRYLAND SALINITY

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ABSTRACT: The paper reviews some of the obstacles to dryland salinity control and compares the advantages and disadvantages of various policy options. It is suggested that taxes per unit of salt emission or subsidies per unit of salinity reduction are theoretically preferred options against which more practical options may be compared. It appears that in more traditional areas of soil conservation, net returns to some components of publicly sponsored programs have been low or negative. It is argued, however, that returns to salinity control programs could be expected to be higher. A review of empirical economic studies of dryland salinity suggests that, in Victoria, there may be scope for alleviating the problem through relatively minor changes in existing farming systems. More drastic approaches such as reforestation may only be required in limited areas.

The problems of dryland salinity, irrigation salinity, and water quality are closely linked—both technically through the hydrologic cycle, and in economic terms through the relationships between resource use and production of agricultural commodities. There are also linkages between dryland salinity, soil erosion and water quality. For these reasons we shall at times group soil problems under the general heading of “soil degradation”. The physical and biological processes involved in the particular case of dryland salinity are described by Peck (1978), and Jenkin & Morris (1983).

The damage caused by salinity is sometimes measured in terms of area of land affected, value of lost agricultural production, and costs imposed through decreased water quality. The estimates of damage in Table 1 have been adapted from Mitchell *et al.* (1978), and Cary *et al.* (1983) and employ 1980/81 prices.

Table 1 indicates that, in terms of the area of land affected and economic losses through reduced agricultural production, the impact of dryland salinity in Victoria is roughly equal to that of irrigation salinity. Both forms of salinity contribute to decreased water quality which is estimated to cost \$7.3 million per annum.

Estimates of economic losses due to salinity are useful in drawing attention to the magnitude of the problem. However, such calculations do not indicate what action should be taken in response to the problem. The costs of controlling salinity may be greater than the anticipated benefits.

The benefits of salinity control may include:

- increased income to some farmers
- decreased expenses to rural, urban and industrial water users
- increased water-based production and recreation, particularly fishing
- an environment more favourable to flora and fauna
- increased forest-based production and recreation
- enhanced aesthetic appearance of landscapes.

The costs of salinity control may include:

- reforestation costs

- costs to farmers of landuse changes
- increased administration costs to public institutions.

The only Australian study that attempts to evaluate all the benefits and costs of dryland salinity control is that by Bennett & Thomas (1982).

We review some of the possible obstacles to the control of dryland salinity and compare the advantages and disadvantages of various policy options. Some empirical economic studies are briefly reviewed, together with the results of analyses conducted by the authors.

REASONS FOR GOVERNMENT INTERVENTION IN SALINITY CONTROL

Almost all production processes managed by man have the potential to cause damage to the environment. Fortunately, it is often in the manager's self-interest to ensure that the damage is avoided by adoption of appropriate practices. However, in the case of salinity—and of other forms of soil degradation and air, land and water pollution—there are several reasons why the firm or manager may not adopt systems and practices which avoid damage to the environment. These reasons have been described previously (Dumsday 1983) and may be summarised as: a, lack of knowledge concerning complex environmental relationships; b, uncertainty concerning the extent to which environmental degradation is irreversible; c, lack of concern for the off-site effects of landuse, such as salting of other land and salinisation of streams; and d, possible divergence between individual and community views of the importance of future costs and benefits. All these factors point to the desirability of public institutions taking an interest in assisting, or requiring, private landholders to control soil degradation.

The next section takes a closer look at the ways in which governments have, or could, intervene to ensure rational use of soil and water resources.

COMPARISON OF POLICY OPTIONS FOR CONTROLLING SOIL DEGRADATION

It may be useful to divide possible policies into two

TABLE 1
ESTIMATES OF ECONOMIC LOSSES DUE TO SALINITY

(A) <i>Loss of Production (Vic.)</i>	
Dryland Salinity	
Cropping Land	27 000 ha affected
Grazing Land	58 000 ha affected
Lost Production (net)	\$5.5 m/annum
Irrigation Salinity	
Kerang Region	75 000 ha affected
Shepparton Region	2 000 ha affected
Lost Production (net)	\$6.0 m/annum
(B) <i>Downstream Effects—Water Quality</i>	
Agricultural (Vic. & S.A. irrigation)	\$2.0 m/annum
Household (S.A.)	\$5.0 m/annum
Industrial (S.A.)	\$0.3 m/annum
Grand Total	\$18.8 m/annum

(Adapted from Mitchell *et al.* 1978; Cary *et al.* 1983)

groups—those that are aimed at overcoming “imperfections” in terms of producer knowledge and capital markets; and those that are concerned with divergences between private and socially optimal use of soil and water resources.

IMPROVING THE AVAILABILITY OF INFORMATION

The first group of policies largely concerns investment in research, education and extension programs aimed at improving the individual farmer's understanding of the impact that soil degradation has on his business. Such programs can probably be easily justified in economic terms, particularly under the conditions of widespread soil degradation that applied in Australia and the U.S.A. in the 1930s and the 1940s and that seem to be re-emerging in the 1970s and 1980s. Even under such conditions it would not generally pay an individual farmer to conduct his own research into degradation problems but, up to a given level of investment, society should benefit by sponsoring research programs for farmers as a group.

Farmers will normally adopt new practices emerging from the above programs if they can be persuaded that their net incomes will consequently increase. However, there may be situations where, for example, the farmer cannot obtain the necessary credit, even at competitive rates of interest. Governments may intervene in such situations to ensure that credit is made available, at competitive rates. The government's role here may consist merely of helping to persuade lenders that the expected net benefits of the investment will enable the borrower to repay the loan.

This group of policies can be aligned with similar policies in other areas of agricultural production. By increasing the rate of expansion and adoption of new technology both farmers and consumers are normally made better off. Generally speaking, the better the income-increasing ability of the new technology, the faster it will be adopted.

The policies to be discussed in the next section may sometimes be used as catalysts to the adoption of new technology. However, we believe that the existence of such policies should more commonly be seen as an admission that well-informed farmers have not found it profitable to adopt a given set of soil conservation practices deemed desirable by public agencies. Also, there is evidence that while some countries have met with considerable success in the “information” area, the performance of policies aimed at closing the gap between private and public “optima”, has been disappointing, despite the expenditure of large quantities of funds (Comptroller General of the U.S. 1977, Williams 1979).

POLICIES FOR CLOSING THE GAP BETWEEN PRIVATE AND PUBLIC OPTIMAL USE OF SOIL AND WATER RESOURCES

In the following discussion policy options are grouped under three headings—taxes and subsidies on soil degradation; taxes and subsidies on inputs and outputs; and direct controls.

Per unit taxes and subsidies on soil degradation

Economists generally regard direct, per unit taxes on emissions of pollutants as the most efficient means of controlling pollution or soil degradation. See, for example, Amihud (1976), Anderson *et al.* (1978), Moffitt *et al.* (1978), and Seneca & Taussig (1979). Such direct taxes are generally advocated as being consistent with the “polluter pays principle”. Critics of this proposal are quick to point out the serious legal, political and technical measurement obstacles to its introduction. To date these obstacles have prevented adoption of the idea in any part of the world to the authors' knowledge.

In the case of salinity problems, taxes could be imposed on salt emissions or “deep percolation” (recharge) of water from dryland agriculture. These procedures would not necessarily entail the difficult or impossible task of directly monitoring and measuring the pollutants at all times, in all locations. A more feasible alternative is to identify relationships between farming systems and salinity for various locations to facilitate indirect monitoring of pollution. Work by Bennett & Thomas (1982), and the authors, amongst others, is developing the necessary relationships. A theoretical treatment of production functions for nonpoint pollution is provided by Griffin & Bromley (1982). They emphasise that such functions would allow “economically efficient policies to be based upon those factors which determine pollution rather than the pollutant itself”.

It is possible that technological developments in soil degradation measurement and modelling, and a continued poor performance of alternative policy instruments will lead eventually to the introduction of soil degradation taxes in some form or other. In the meantime they provide a useful basis for comparison with other policy instruments.

In theory, subsidies per unit reduction in soil degradation have the same effect as taxes per unit of remaining soil degradation, in terms of closing the gap between social and private optimal rates of soil utilisation. However, while taxes initially transfer income

from farmers to the community, subsidies do the opposite. In addition, subsidies may have two undesirable effects. First, they may not provide clear incentives for the development of least-cost systems of soil conservation. Secondly, they may actually encourage producers to expand cropping on to even more susceptible land in order to capture more subsidy (Baumol & Oates 1975).

Taxes and subsidies on inputs and outputs

Subsidies for soil conservation works and land management practices have probably been the most common form of public intervention up until now. Low interest loans and income taxation concessions for soil conservation works also come under the heading of subsidies on inputs.

The application of taxes or subsidies to inputs or outputs has at least three possible disadvantages. First, soil degradation is normally the result of interacting management factors and there is seldom good correlation between any one factor and the degree of soil degradation. Under such circumstances it is difficult to calculate the least-cost tax or subsidy package. Secondly, as in the case of direct subsidies per unit reduction in soil degradation, there is a danger of input subsidies leading to increased degradation as farmers find it profitable to cultivate more susceptible land. Thirdly, it may be quite difficult, in the case of input subsidies, to provide a continuing incentive for reducing the costs of soil conservation by the application of new technology.

The application of input taxes does not suffer the last two disadvantages. However, it is difficult to imagine an efficient input package for dryland salinity other than perhaps imposing additional taxes (or withdrawing current subsidies) on tractor fuels which, in some regions, would swing cost advantages away from fallowing in favour of reduced tillage systems. Taxes on conventional cultivation equipment or subsidies on minimum tillage equipment would be an alternative but the effects would take place gradually as farmers replaced their machinery. Increases in wage rates and oil prices relative to the prices of other factors of production like pesticides may have already provided incentives for producers to move towards minimum tillage systems. By maintaining plant cover for longer periods compared with traditional practices, such systems offer reduced soil erosion and reduced deep percolation of rainfall to groundwater. Crosson (1981) reviews a number of technical and economic issues relevant to comparisons between conventional and minimum tillage systems.

Taxes and subsidies on outputs have not been implemented specifically to meet soil conservation objectives. It would be possible to tax crop products (Seitz 1981) or subsidise pasture products but, again, these would be rather blunt instruments for controlling soil degradation. Schultz (1982) has pointed out that taxes on crops would penalise all crop producers regardless of whether or not their farms were contributing to soil degradation and water quality problems. However, it would be useful to remind policy makers from time to

time of the implications for soil degradation on some farms of, for example, providing export incentives for crop production.

Direct controls

Direct controls include regulation; zoning; or prohibition of various forms of land use; or resumption of land in order to meet specified levels of soil conservation or salinity management.

Direct controls normally have several disadvantages. First, they tend to require a great deal of information on relationships between management practices and soil degradation if the controls are to operate efficiently. Second, they are often inflexible in the face of changes brought about by new technology. Third, the standards are usually arbitrary in economic terms, no attempt being made to compare the benefits and costs of more stringent standards with those for less stringent standards. Fourth, direct controls often do not allow the individual farmer enough discretion in choosing combinations of management practices and land uses to meet soil conservation objectives.

In practice, most governments have used a combination of measures from the two latter options to combat soil degradation. However, it is clear from Australian and U.S.A. experience that only partial success has been achieved (Comptroller General of the U.S. 1977, Department of Environment, Housing and Community Development 1978). Producers have tended, for example, not to maintain terrace systems or contouring practices and have even been permitted at times to use conservation funds for production activities which lead to overall increases in soil degradation.

RESULTS FROM EMPIRICAL ECONOMIC STUDIES

To economists, the degree of control over soil degradation to be desired depends on comparisons of benefits and costs, whether from an individual or community point of view. Some of the difficulties in performing these comparisons have been noted previously (Dumsday 1983). The diffuse, non-point nature of soil degradation processes and their effects in terms of water pollution and agricultural productivity further adds to the difficulties for benefit-cost analysis.

Despite the above difficulties, a large number of economic evaluations have been completed in the U.S.A. and, to a lesser extent, in Australia (Dumsday 1983). Broadly speaking, these studies show low or negative social returns to public programs aimed at reducing soil degradation rates below those incurred by profit-maximising individuals. However, they also show that, while some individuals may suffer significant income losses as a result of programs for soil conservation, the net social costs of significantly reducing soil degradation are likely to be low for efficiently run programs. Given the uncertainties discussed earlier "society" may be prepared to accept low or even slightly negative returns for such programs.

The studies referred to above mostly concerned themselves with more "traditional forms of soil de-

gradation such as sheet erosion in cropping areas. There are few comprehensive benefit-cost analyses of dryland salinity control programs, either in Australia or overseas. In our view the social returns from salinity control (over and above those concerned with the informational aspects discussed previously) may be higher than those for traditional forms of degradation because of the relatively greater importance of off-site versus on-site effects. The on-site effects of sheet erosion, for example, are often large and tangible in relation to the total social consequences of such erosion, so it is often in the individual's interests to do something about the problem. In contrast, the on-site effects of salinity processes initiated by a given form of land use may be small in relation to their off-site effects on streams or on land owned by other individuals.

As mentioned in the introduction, the only Australian study (and probably the only study in the world) that attempts a comprehensive evaluation of the benefits and costs of dryland salinity control is that reported by Bennett & Thomas (1982). This study took a multi-disciplinary approach to the evaluation of proposals for salinity control in wheat-growing areas in the Murray catchment of Western Australia. Table 2 summarises some of the results of the study and demonstrates that the evaluation was quite broad—capturing the benefits and costs of agricultural production, agroforestry, forestry, mining, recreation, and water storage.

On a catchment basis the results suggest that, compared with current landuse, economic returns could increase and stream salinity levels decrease, by increasing the area devoted to national parks, mining, and agroforestry, while reducing the area devoted to hardwood forest, and traditional agriculture. A study employing similar methodology to that of Bennett and Thomas is being conducted in Victoria by the authors.

A study reported by Greig & Devonshire (1981) was

based on a cross-sectional regression analysis of 56 Victorian catchments. They found that levels of stream salinity across all catchments were satisfactorily explained by a function of the form:

$$S = f(T, R, P)$$

where S = mean stream salinity (mg/L, total dissolved salts)

T = percentage of catchment covered with forest

R = Percentage of catchment on sedimentary rock

P = annual average rainfall (mm).

By applying this function to the Loddon catchment in Northern Victoria, Greig and Devonshire were able to show that the cost, through increased stream salinity, of additional forest clearing was likely to be about \$88 per hectare, or a perpetual annuity of \$4.40 per hectare. They suggested that these sums could be levied as clearing taxes—\$88 per hectare at the time of clearing or \$4.40 per hectare annually in perpetuity from the time of clearing onwards. Hodge (1982) has suggested that one of the schemes for combating dryland salinity in Australia could involve government imposition of transferable quotas on the extent to which individuals are permitted to clear their land.

In a farm level study, we have taken a simulation modelling approach to the economic evaluation of dryland salinity control in Northern Victoria. The simulation model operates on a daily basis and incorporates relationships between site-specific characteristics (such as soil type, topography and weather) and annual crop and pasture yields from farming systems employing various rotations and tillage practices.

The amount of daily deep percolation of water beyond the rootzone was taken as a surrogate measure of the salinity-inducing characteristics of different farming systems through their influence on the phenomenon

TABLE 2
THE W. A. MURRAY CATCHMENT STUDY

	Existing Land Use	Allow Mining	Construct One Dam ^a	Allow Agroforestry
<i>Land Assignment (ha × 10³)</i>				
National Parks	0	42	25	25
Forests	320	258	536	205
Agriculture	343	343	12	5
Mining/Forest	0	0	12	6
Mining/Agriculture	0	20	8	14
Agroforestry	0	0	0	338
Flora and Fauna Reserves	0	0	65	65
<i>Net Present Value (\$ × 10⁶)</i>				
Total NPV (7%)	100	435	359	446
River Flow (m ³ × 10 ⁶)	312	328	177	177
Salinity (ppm NaCl)	1 226	1 230	452	457

(Adapted from Bennett and Thomas 1983, Tables IV-6, IV-8, and IV-13).

^a Salinity constrained to 500 ppm TDS.

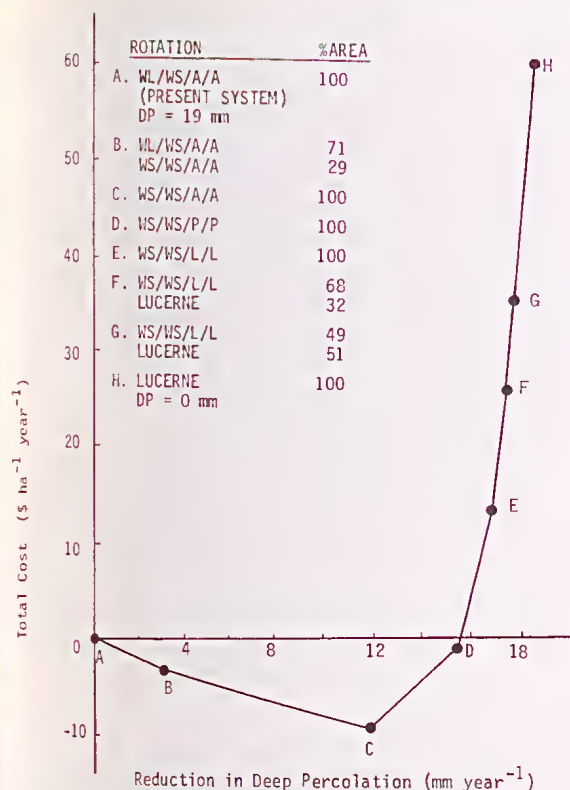


Fig. 1—Total costs of reducing deep percolation—Kamarooka.

of groundwater recharge. The model was run for approximately 40 years using data for Kamarooka (wheat-sheep systems) and Axe Creek (grazing systems) in Northern Victoria.

The results from the simulation model were averaged and passed to a linear programming model to select "best" farming systems given relative commodity prices and variable production costs. Farming systems commonly practised in the two areas were then selected as the *base* systems against which alternative systems showing reduced deep percolation of water were compared. These analyses provided information on the important relationship between farm income and reduction in deep percolation. The results of the analyses are summarised in Fig. 1 for Kamarooka and Fig. 2 for Axe Creek.

In Fig. 1, WL is wheat, long fallow; WS is wheat, short fallow; A is annual pasture; P is perennial pasture; and L is lucerne. For Kamarooka, the current farming systems are estimated to result in average annual deep percolation of 19 mm. This figure can be reduced by about 12 mm per annum while *increasing* income, by substituting short fallow for long fallow in the rotation (system C). However, further reduction in deep percolation implies rapidly increasing costs to the operator.

The suggestion that farmers are currently opting for a farming system that is sub-optimal in terms of their net income warrants closer examination. The authors believe that they have made realistic assumptions concerning price relationships and input-output coefficients.

However, the results are yet to be extensively tested under field conditions. Technical difficulties in establishing and managing the suggested farming systems may need to be overcome before widespread adoption can be expected.

It can be shown using marginal cost analysis that, while the equivalent of a tax or subsidy of about \$2.30 per mm deep percolation per annum would be required to persuade the operator to move from system C to system D (giving 84% reduction in deep percolation from base levels), it would be necessary to issue a tax or subsidy of about \$28.50 per mm per annum to move to system H involving all lucerne and no deep percolation.

For Axe Creek, current farming systems are estimated to result in average annual deep percolation of 34 mm. Any reduction from this figure would involve increasing costs to the operator. However, the increases are not as rapid as those for Kamarooka. The equivalent of a tax or subsidy of about \$0.20 per mm per annum should persuade the operator to move from system A (annual pastures) to system C which employs perennial pastures on 70% of the property and lucerne on the remaining 30%. At this point, deep percolation is reduced by about 92% from base levels.

Physical or engineering measures for control of dryland salinity such as river flushing, surface and underground drainage, and groundwater pumping were not evaluated by the authors. Such measures may be useful in some dryland situations. However, as Jenkin & Morris (1983) have indicated, they are mainly applicable to control of salinity in irrigation systems.

Some feasible landuse activities such as agroforestry or reforestation were not included in the above analyses and are to be considered in later work. However, these activities imply major changes to farming systems in

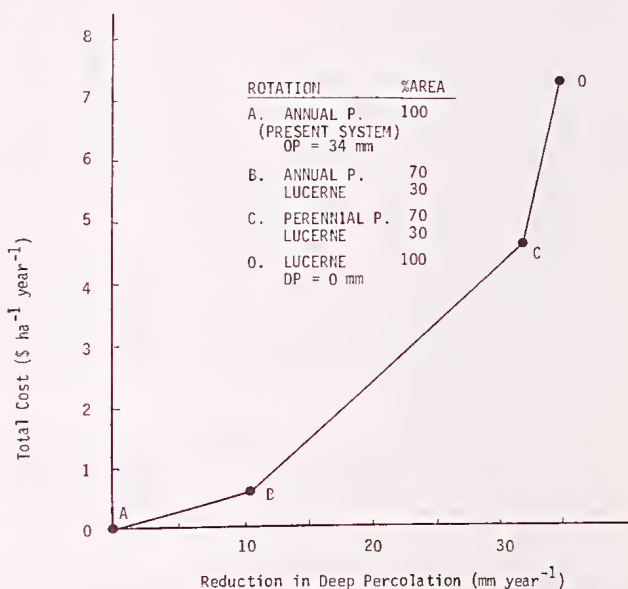


Fig. 2—Total costs of reducing deep percolation—Axe Creek.

Northern Victoria and may not be any more profitable than the lucerne-based activities already examined. This does not necessarily mean that further clearing of existing forest or scrub is warranted on economic grounds. Indeed, the work of Greig & Devonshire (1981) described earlier indicates that any existing public incentives applied to clearing, such as business deductions or investment allowances for income taxation purposes, should probably be revoked.

SUMMARY AND CONCLUSIONS

It is clear that dryland salting is an important problem in Victoria, causing losses in agricultural production to the value of about \$6 million per annum. To these losses must be added the costs of decreased water quality to Victorian and South Australian consumers.

Solutions to the problem are not so clear. Lack of knowledge concerning the physical processes involved; lack of concern for the off-site effects of land-use; and possible divergence between individual and community views of the importance of future costs and benefits all present obstacles to the rational use of land.

The paper compared several groups of policy options for controlling dryland salinity. It was suggested that the traditional research and extension roles of public agencies should continue to bring benefits to society by improving the availability of knowledge and increasing the rate at which improved technology is adopted by agricultural producers. In the simplest case, the causes and effects of dryland salinity are confined to land under the control of one individual or firm. In such cases it should be possible to persuade the landholder that his income will be improved by adopting technology aimed at controlling dryland salting.

Unfortunately, the causes of dryland salting are normally remote, in terms of time and place, from its effects. In such cases, fully informing the perpetrator of the actual or potential effects of his actions may not lead him to "mend his ways". Under such circumstances economists prefer the imposition of direct, per unit of pollution taxes on the perpetrator—a policy option which recognises the "polluter pays principle". This principle is difficult to apply in the case of dryland salinity, although it provides a useful basis for comparison with other policy options.

Subsidies for soil conservation works and land management practices have been the most common form of public intervention up until now. The subsidies are usually offered as part of voluntary programs which are often characterised by short-term success and long-term disappointment as farmers gradually lose interest for various reasons.

Direct controls on landuse also have potentially serious disadvantages in terms of unnecessarily draconian restrictions of landholders' managerial freedom and the arbitrary nature (in economic terms) of technical "standards" that may be established.

Despite the above difficulties, a review of some empirical economic studies suggests that there are some useful steps for public agencies to consider. Firstly, the

agencies should closely examine any remaining incentives for clearing forest or scrub, such as are provided by income taxation allowances. (Some of these incentives are probably hang-overs from a past in which increases in agricultural exports were seen as the main avenue for improving the "balance of payments".) Secondly, quotas or taxes on further clearing could be considered. Finally, there appears to be scope for significantly alleviating the problem of dryland salinity through relatively minor changes in existing farming systems, involving modification of fallowing practices and introduction of deeper-rooted perennial grasses and legumes. More drastic approaches such as reforestation or agroforestry may only be required in limited areas.

ACKNOWLEDGEMENTS

The work reported here was partly supported by grants from the Soil Conservation Authority, Victoria and the Australian Water Resources Council. Thanks are due to G. W. Edwards, La Trobe University, W. A. Papst, Soil Conservation Authority, Victoria, and an anonymous referee for comments on a draft version of the paper. An earlier version of the paper was presented at a symposium on Salinity in Victoria (Dumsday 1983).

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LUNETTES AS INDICES OF HYDROLOGIC CHANGE: A REVIEW OF AUSTRALIAN EVIDENCE

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ABSTRACT: A variety of transverse dune types occurs on the eastern margins of lake basins across southern Australia. Known collectively as 'lunettes', these range in composition through quartz-rich, sandy clay, gypseous clay to nearly pure gypsum. The origin of the pure quartz dunes formed under lake-full conditions, is distinct from that of the clay or gypsum-rich variety which formed by deflation from adjacent lake floors.

In the lunette forming processes the role of salts and groundwater is critical. Descriptions of modern examples from Texas provide analogues of clay dune building that affected hundreds of small basins across southern Australia during late Pleistocene time at the height of the last glacial episode.

Modern clay deflation examples from Lake Eyre and Lake Tyrrell confirm the role of salts especially halite and, on the edge of Lake Tyrrell, thenardite, in providing the active efflorescent mechanism which physically breaks the near surface gypseous clays into a soft fluffy pelletal layer preparatory for deflation.

The deflationary process, associated with strong frontal systems, raises large dust clouds today from some playa floors involving both suspension and traction loads. Such conditions, favoured by long droughts and strong winds, were intensified during late Pleistocene time when the final and most dramatic phase of regional clay dune (lunette) building occurred across southwestern to southeastern Australia. In this way, the variety of ancient lunette forms, when set beside modern examples both here and overseas, provide a most instructive window to help interpret the legacy of ice age hydrologic and climatic processes that affected large inland regions of the Australian continent.

In 1939 E. S. Hills produced a major paper in these Proceedings dealing with the physiography of north-western Victoria. That paper was noteworthy for two reasons. It assembled for the first time a huge amount of topographic detail drawing upon records from railway and State Rivers channel surveys; in doing so, it produced the first topographic map of the region, highlighting the north-south ridges and other features. Secondly, it provided the first geomorphic analysis of a region which, perhaps above all others in Australia, possesses a diverse and distinctive array of peculiarly Australian landforms, legacies of complex Quaternary environmental changes which were as challenging to Hills in 1939 as they are productive to Quaternary scientists today.

In recording the succession of buried soils within longitudinal dunes near Ouyen, Hills related their origins to past climatic oscillations (soils during humid periods, dune growth in arid phases). Thus he anticipated those cyclic climatic oscillations which later work is only now beginning to clarify. Additionally, in drawing particular attention to the presence of clay-rich transverse dunes on lake margins, he singled out the enigmatic landforms which he went on to name '*lunettes*' (Hills 1940).

Subsequent work involving stratigraphic, chronologic and archaeological studies of lunettes through southeastern Australia has shown them to be rich repositories of the ancient history of climate, animals and Man. In this essay I wish to explore some of the many facets of lake-lunette studies which have burgeoned since the pioneering work of Hills in 1939.

PREVIOUS WORK

On 24 July 1836, Major T. L. Mitchell, on his

famous journey through the river systems of south-eastern Australia, noted in his diary:

I proceeded to examine and survey some of these remarkable lakes. On the margin of one of them . . . a green hill of rather singular shape rose to a considerable height, above the surrounding country. I found the water in the lake beside it, shallow and quite salty . . . This was surrounded by a narrow beach of soft white mud or clay . . . The green hill was the highest of several semi-circular ridges, forms that may perhaps be better understood by the accompanying plan. There was a remarkable analogy in the form and position of all these hills; the form being usually that of a curve, concentric with the lake, and the position invariably on the eastern or north-eastern shores, a peculiarity I had previously observed, not only in the lakes near the banks of the Murray, but also in others of the Murrumbidgee and Lachlan, where the ridge consisted of red sand . . . (Mitchell 1839, pp. 190-191).

Mitchell's description and map (Fig. 2), which were remarkable for their clarity and attention to detail, provide us with the first record of these unusual lake-shore dunes. But for almost the next 100 years, these landforms escaped the attention of Australian geomorphologists.

As so often happens in science, the first systematic observations were made almost simultaneously by two people; Harris (1939) a school teacher at Echuca described loam ridges on the shores of Lake Cooper complex while Hills (1939, 1940) drawing on examples from the Mallee and Kerang set out the systematic description.

From the succession of loam ridges on the shores of L. Benjeroop, Hills (1939) noted that each successive

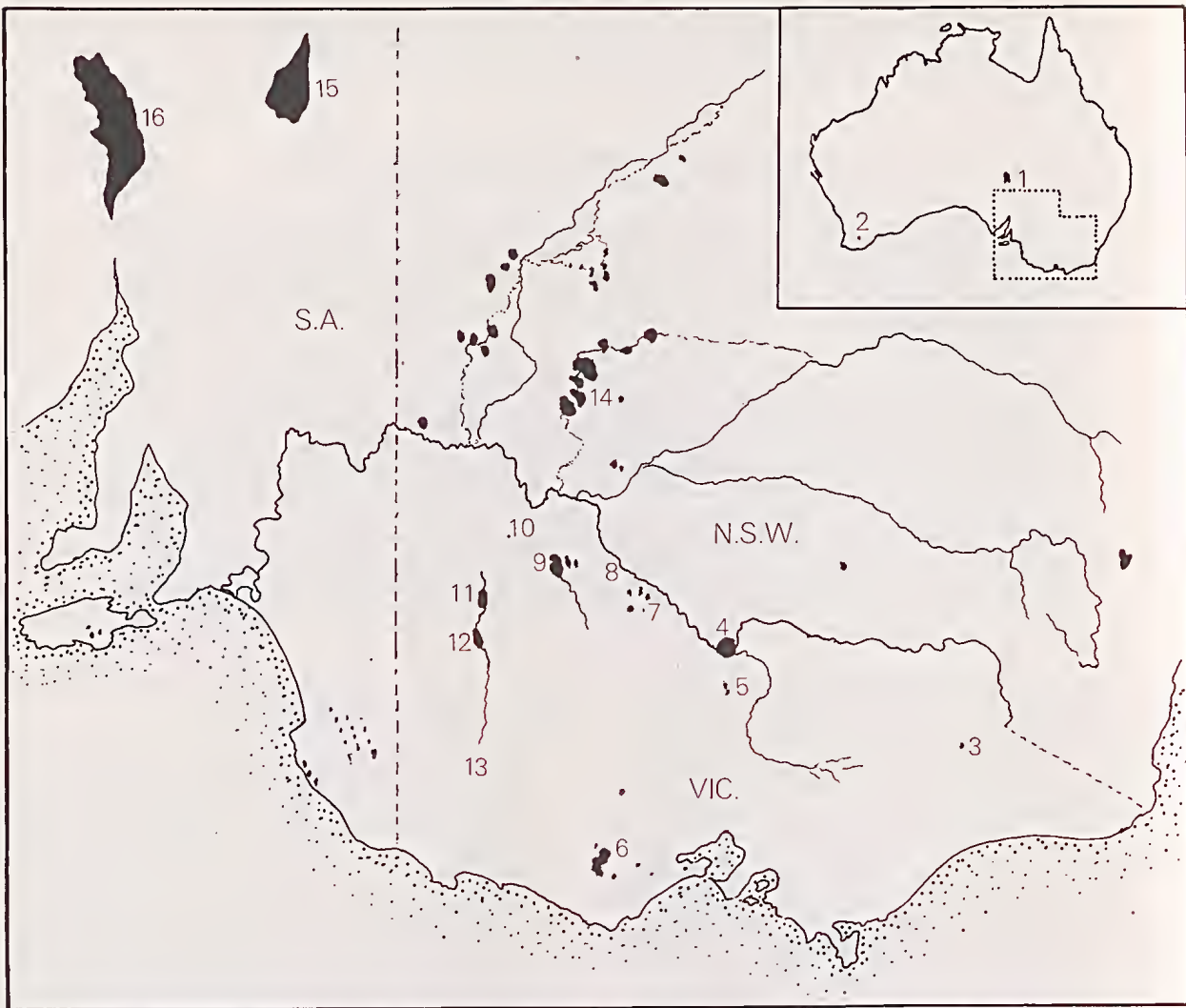


Fig. 1—Location map of sites mentioned in text. 1, Lake Eyre; 2, Wagin Lake; 3, Lake Omeo; 4, Barmah, Echuca, Lake Kanyapella; 5, Lake Cooper; 6, Lake Corangamite; 7, Kerang, Lake Wandella, Benjeroop; 8, Swan Hill; 9, Lake Tyrrell; 10, Ouyen; 11, Lake Albacutya; 12, Lake Hindmarsh; 13, Mitre Lake, Mt. Arapiles; 14, Willandra Lakes—Lake Garnpung, Lake Mungo and Wall of China, Lake Outer Arumpo, Chibnalwood Lakes; 15, Lake Frome; 16, Lake Torrens.

phase was built inside the perimeter of the last; all were on the margin of successively lower lake levels. Thus he established an important relationship between clay dune occurrence and water-level, a relationship which is relevant to many aspects of dune origin. The difficulty of obtaining saltation grains from the lake floor together with the apparent water-level control, led Hills to postulate a mechanism of downwind flocculation of fines by salt spray to produce a local concentration of clay-sized sediment. But he also acknowledged the probable importance of other processes, particularly that of pelletal concentration by deflation from lake floors as demonstrated in Texas (Coffey, 1909). But at that time data from the Texan examples was insufficient to permit detailed comparison to be drawn with the Australian fossil examples (Hills 1940, p. 5).

In the same year that saw the publication of Harris' and Hills' observations, Baldwin, Burvill and Freedman (1939) published the first soil survey in the Kerang district showing the local distribution of clay dunes and their associated soils. They noted that soils on the 'red sand hills' (soil type 4) were of lighter texture and contained significantly more sand than the surrounding heavy clay plains. The profiles had 'reached an advanced stage of maturity' indicating stability for considerable periods, evidence for the relict nature of these forms.

Stephens and Crocker (1946) presented the first regional account of lunettes throughout southern Australia. They described occurrences from Tasmania, Western Australia, South Australia, Victoria and southern New South Wales and provided detailed analyses of the range of textures in vertical profiles

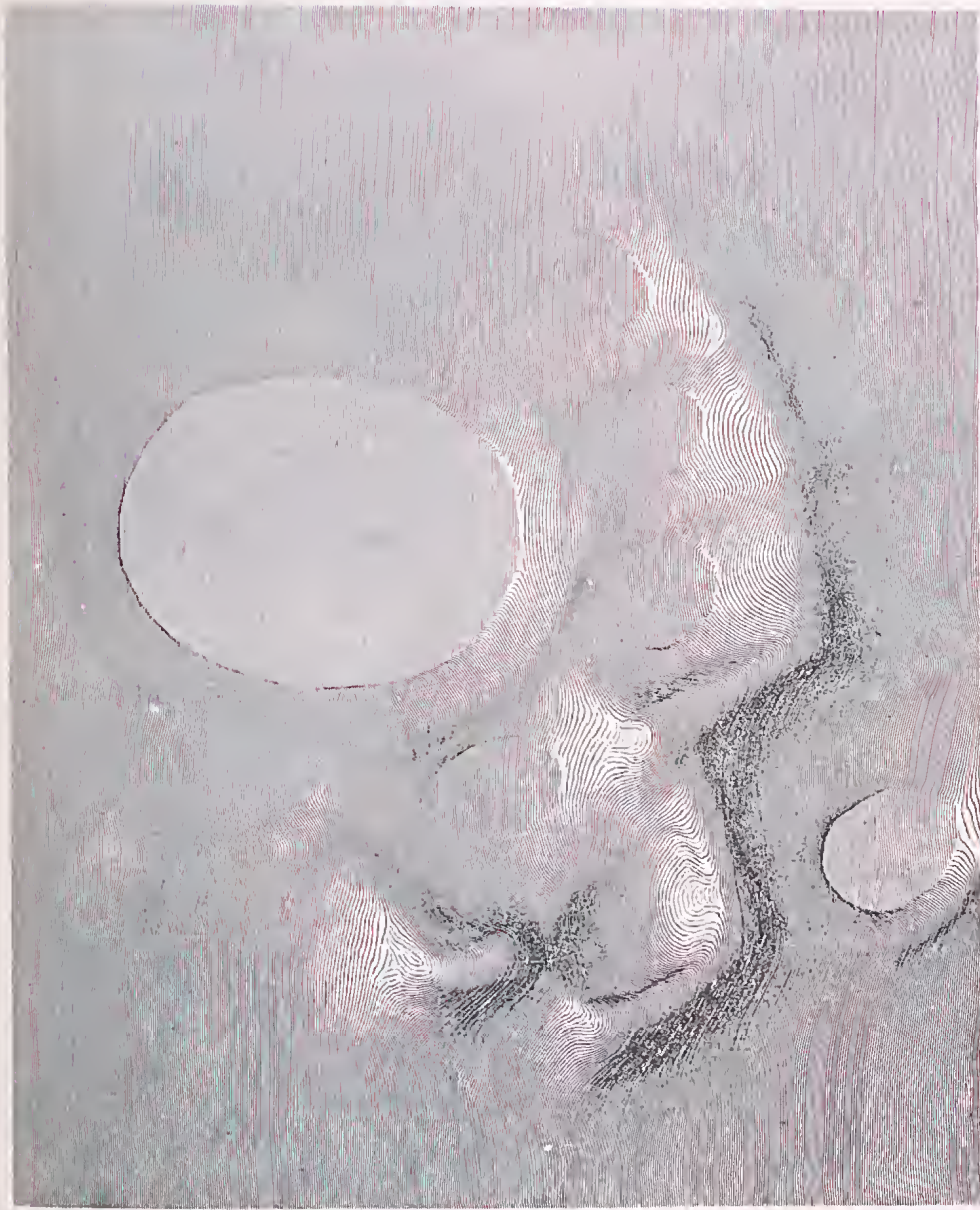


Fig. 2 – The first map of lunettes ever made. Greenhill Lake near the Grampian Ranges, western Victoria, surveyed by Major T. L. Mitchell in 1836. Map from Mitchell, 1839.

through representative dunes at various sites. They drew attention to the significance of the wide range in textural composition from coarse sands at Wagin Lake, Western Australia, to the dunes composed mainly of clay as at Kerang, Victoria. They noted some of the difficulties in the spray precipitation hypothesis especially in its failure to account for the coarse sand components. They revived the lake floor deflation theory proposed initially by Harris (1939) pointing out that it provided a satisfactory hypothesis for the textural variation within the sediments, a view supported later by Bettenay (1962). The lunette 'composition is governed by the nature of the material present on the surface of the dry lake floor,

and immediately to the windward . . .' (Stephens & Crocker 1946, p. 309). They saw no cause to associate lunette building with the presence of water as claimed by Hills from the multiple lunettes at L. Benjeroop. All lunettes were therefore interpreted as evidence of aridity. In supporting the dry lake deflation hypothesis, Stephens and Crocker did not attempt to explain why similar features rarely form today.

Sprigg (1979), recording lunettes on the continental shelf, emphasised their relict character and age of formation associated with glacial low sea-levels.

For many years the problem of lunette formation and their environmental significance received scant at-

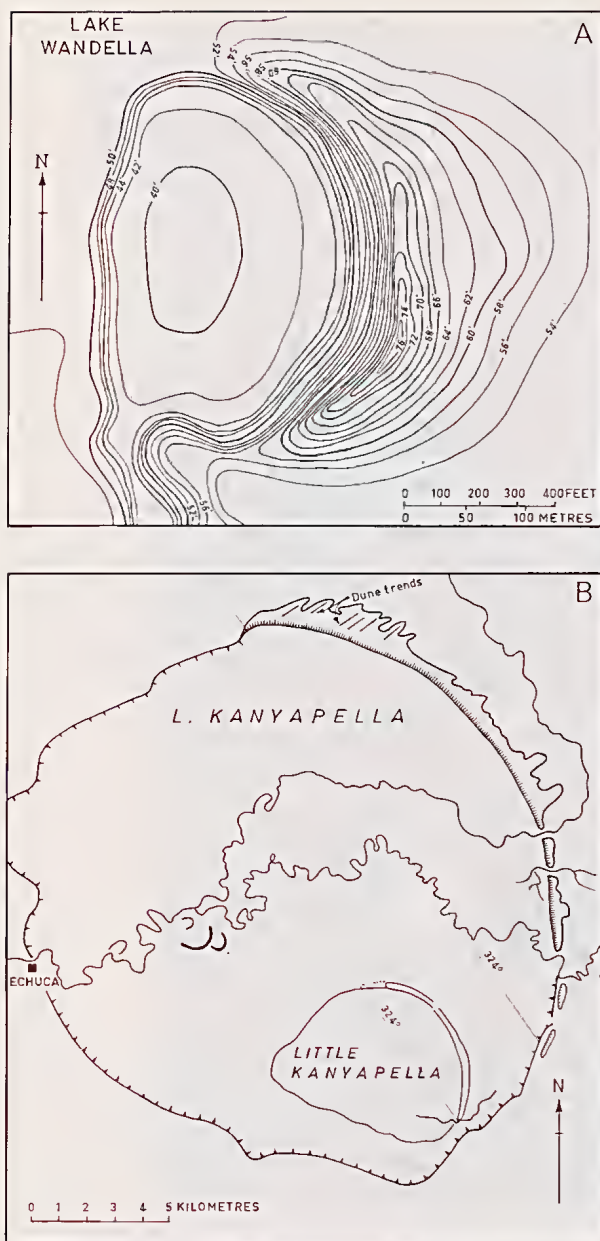


Fig. 3—Typical lunette forms in northern Victoria.
A, clay lunette at Wandella, near Kerang.
B, quartz sand lunette at Kanyapella near Echuca.

tion. Bowler and Harford (1966) in describing the lunette-lake system in the fault-angle depression near Echuca (L. Kanyapella), postulated a high water level origin for the coarse textured sand lunette in opposition to the dry lake theory. Currey (1964) had previously reported the modern deflation of wave transported *Coxiella* shells into a dune on the eastern shores of L. Corangamite, western Victoria, contributing to lunette formation. Thus lunette development is considerably

more complex than in the relatively simple dry lake theory advanced by Stephens and Crocker.

In a short account of Australian lunettes Bowler (1968) stated that two distinct types of lunettes exist, the formation of which must be considered separately. Firstly, the quartz sand lunettes with low clay content similar to that at Echuca have developed by deflation from active lakeshore beaches. A similar explanation may also apply to the coarse textured Wagin Lake lunette, Western Australia (Stephens & Crocker 1946, p. 306) and to that with bedded '*Coxiella* shells and quartz grit' shown in section by Bettenay (1962, plate 1). Secondly, those with high percentages of clay were ascribed to deflation from partially exposed lake floors during periods of low water level in a manner similar to that described from Texas (Huffman & Price 1949, Price 1963). Campbell (1968) correctly emphasised the importance of water but went on to relate *all* lunettes to sediment transport by waves preparatory to deflation. She suggested (p. 107) that clays as well as sands might be related to derivation from beaches, an observation which is at variance with observed modern clay deflation.

An earlier review (Bowler 1973) summarised the main sedimentary characteristics of clay-rich lunettes. I propose to discuss here the evidence now available relating to the conditions under which they form, and their hydrologic and climatic implications in the broad context of Quaternary changes in Australia.

QUARTZ AND CLAY DUNE COMPARISON

Throughout southeastern Australia examples of quartz and clay-loam ridges occur often within the same region and sometimes even on the margins of the same basin. We may contrast the regular topographic expression of the clay-rich forms exemplified by Lake Wandella (Fig. 3A) with the irregular hummocky topography, particularly on the downwind margins of quartz dunes as at Lake Kanyapella near Echuca (Fig. 3B; Bowler & Harford 1966). The sedimentary contrast reflected in the different topographic expression is itself reflecting different origins.

The presence of coarse, well-bedded beach sands with low angle lake-ward dips exposed in sand quarries on the road between Echuca and Barmah provides positive evidence of dune construction from relatively high energy beaches during lake-full conditions (Bowler 1980, fig. 3.13). A textural gradient from coarse to fine away from the beach towards the basin centre demonstrates that the dune sands could not have originated by deflation from exposed lake floor. Instead, they formed from beaches in the same way that foreshore dunes form in many coastal situations today (Fig. 4A).

In several important ways the clay lunettes differ topographically from the normal littoral foreshore quartz dunes (Fig. 4B). The latter characteristically have steeper lee slopes reflecting the development of steep down-wind sandspile faces.

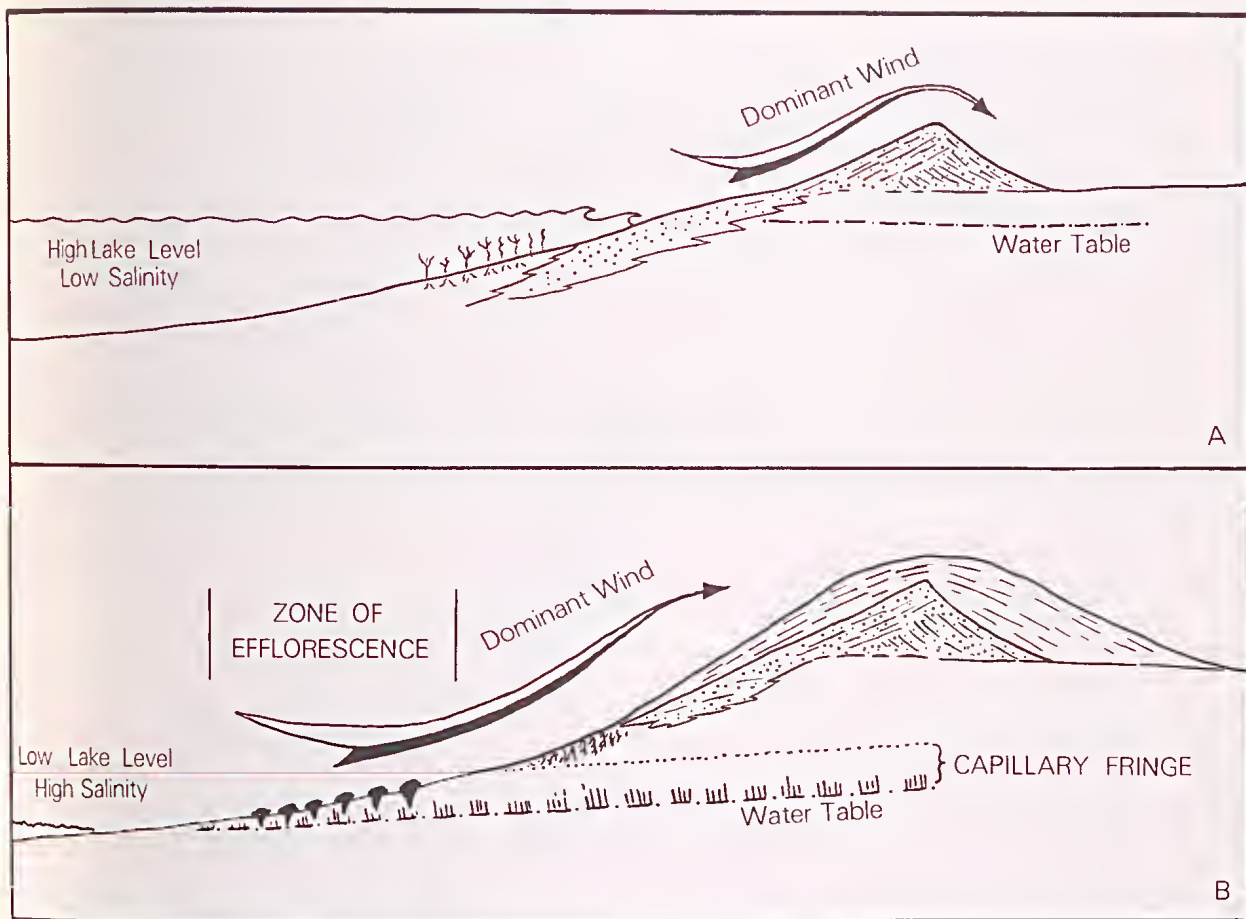


Fig. 4—Cross-sectional diagrams showing the manner of formation of quartz lunettes compared to typical clay-rich lunettes.

A, lacustral conditions; low salinity, deep water environments produce quartz beaches from which transverse quartz dunes formed.

B, relatively arid conditions; surface water deficit results in seasonal exposure of salt flats permitting efflorescence of salts from underlying watertable. Strong winds transport pelletal clays and associated salts to lake margin forming saline clay dune (from Bowler 1980).

This is reflected in cross-bedding as in the L. Kanyapella dune or in the quartz sand component of the Walls of China (L. Mungo) and L. Albacutya lunettes. The clay lunettes on the other hand often possess steep inner, windward slopes and low gentle leeward gradients (see Fig. 3; Hills 1940). This is in part a reflection of their internal structure in which low angle bedding is characteristic. Beds consist of alternate quartz-rich or clay-rich sands from 2 to 30 cm thick at L. Garnpung and L. Albacutya, or as minute laminae a few millimetres thick as on the Walls of China. The angles of deposition are almost always less than 15° on both inner and outer slopes; steep avalanche bedding and cross-set laminae are rarely developed. Thus the clay dunes in their topography and especially in their structure are

distinct from quartz dunes where saltation movement results in sand-piling and development of slip faces.

ORIENTATION

The orientation of lunettes on the eastern side of lakes in southern Australia is consistent with the trend of associated east-west linear dunes reflecting the controlling influence of the westerly winds (Hills 1939, Smith, Herriot & Johnston 1943).

A chord joining the 'horns' of the lunette may be used as a measure of orientation. Another measure is a line which passes through the centre of the lake and bisects the lunette into equal parts. This axis of symmetry will intersect the chord approximately at right angles in symmetrical lakes but not in asymmetrical

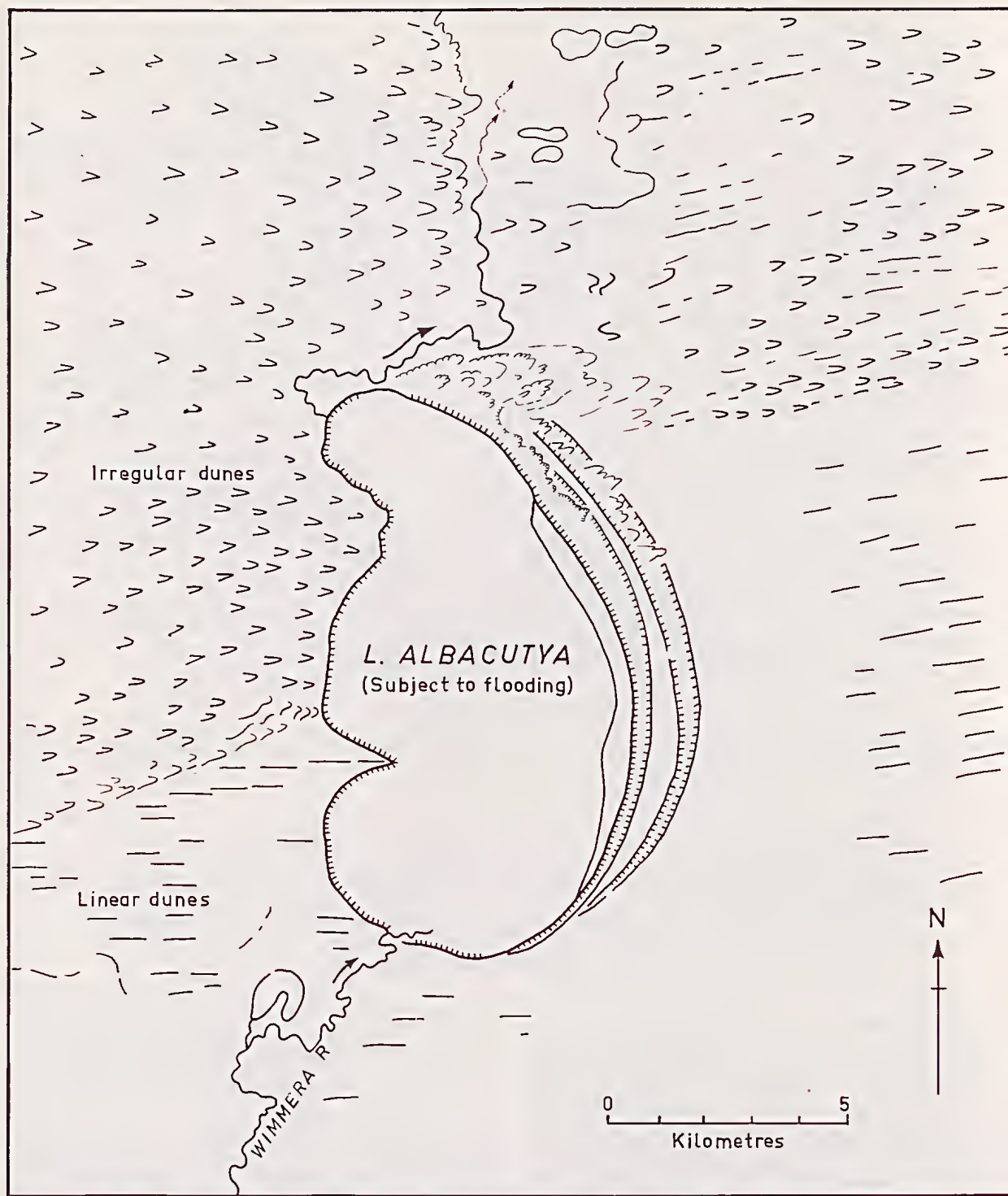


Fig. 5—Map showing the geomorphic setting and features of Lake Albacutya. Note multiple lunette ridges with irregular sub-parabolic lobes of quartz-rich dunes extending downwind from northern margin.

basins. The axis of symmetry which also intersects the lunette at its highest point reflects the direction of the controlling wind regime.

When the orientation of the quartz-rich and clay-rich facies are independently measured, several important features emerge. In the quartz-rich lunettes the ax

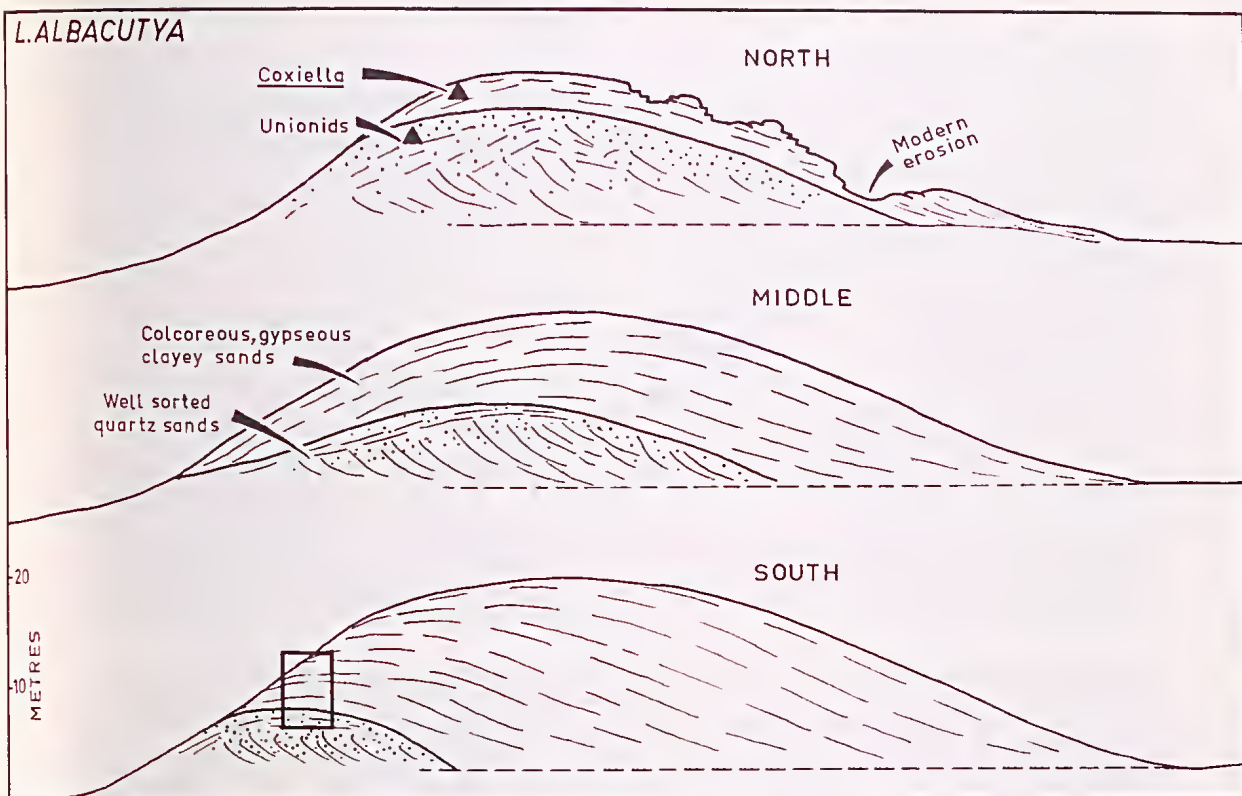


Fig. 6—Stratigraphic sections through inner lunette, L. Albacutya. In the three sections from north to south, the clay blanket thickens reflecting the asymmetric deposition of the quartz and clay members, typical of lunettes of the compound type.

of symmetry usually have a northeasterly orientation parallel to the trends of small parabolic blowouts which sometimes develop on the lunette's outer margin. In the clay-rich dunes the axes of symmetry are usually east-west throughout the Murray Basin.

In the sand lunettes of L. Kanyapella and Little Kanyapella at Echuca, the axis of symmetry has a bearing of 63° compared to approximately 90° for the clay lunettes near Kerang (Fig. 3). Furthermore where linear or Mallee dunes are associated with clay dunes as near Swan Hill, the lunette axes are parallel to the linear trends.

The variation in orientation between the lakeshore quartz and clay components may be found within the sequence on a single lake. On L. Albacutya (Figs 5, 6) the upper blanket cover of clay-rich sediment asymmetrically overlies an earlier quartz-sand component in the inner lunette. On the northern end, the high dune consists of quartz sand. Further south the clay blanket thickens until near the southern end almost the entire dune is composed of the clay component. Thus the quartz sand component has its most prominent development in the northeastern quadrant as at Kanyapella while the later clay-rich blanket has a preferred southeasterly orientation.

This divergence in the disposition of quartz and clay dunes is probably the result of several factors: 1, the

orientation of lakeshore beaches which provided the sand source; 2, the direction of the main dune-building winds which do not necessarily coincide with the most effective beach-building winds, and 3, the control of clay dune growth by winds of a particular season.

Discussion of these factors is deferred until the clay-dune building processes have been clarified.

TERMINOLOGY

In choosing the term *lunette*, Hills was drawing attention to two aspects that differentiate these distinctive features from other types of dunes. Firstly, their clay-loam composition placed them in a special category. Secondly, their plan outline with 'horns' facing into rather than away from the prevailing winds imparted a distinctive shape. Finally, their cross-sectional profiles, commonly asymmetric with the steepest face on the windward rather than lee side, stands in marked contrast to barchan type dunes formed by mobile quartz sand with avalanche bedding on the steep lee-sides. These distinguishing elements of composition and form were implicit in the definition of the new landform.

For later workers identifying and using these features several problems arose. In the first stages of mapping, especially at the photogrammetric stages, it is the distinctive morphology which is observed and interpreted. Detailed field examination is necessary to deter-

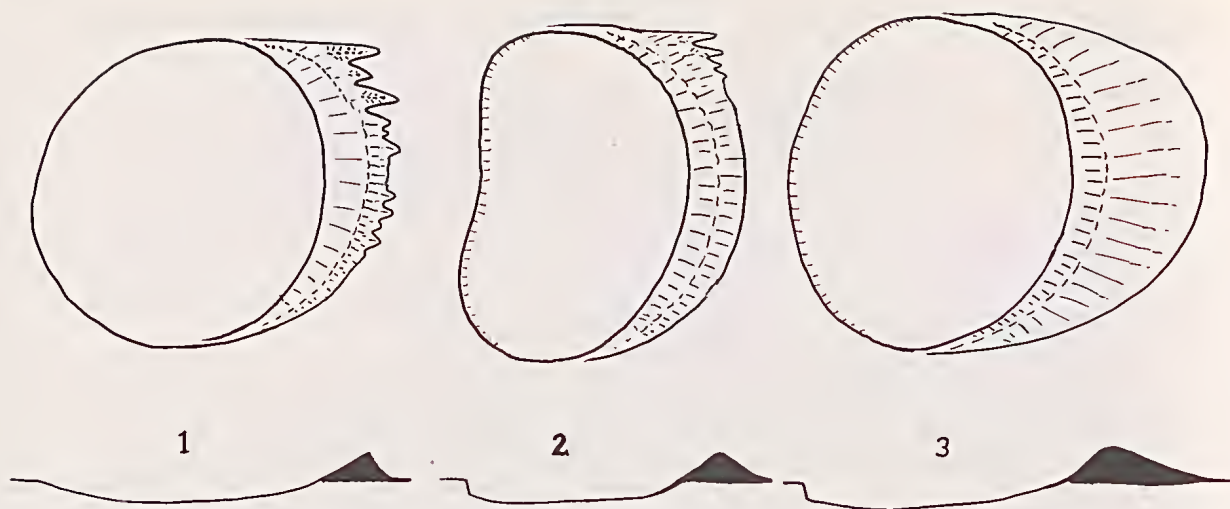


Fig. 7—Plan and section expression of typical basin-lunette associations.

1, quartz foredune, asymmetric with steep leeward slope, often with elongate, sub-linear forms migrating downwind from lee margin. Characteristically no groundwater controlled cliff on upwind margin. Typical example, L. Kanyapella—Fig. 3B.

2, Impure quartz lunette, may be of compound type (quartz core with clay-rich blanket cover). Nearly symmetrical in section, upwind cliff provides evidence of slope retreat controlled by groundwater outcrop zone either past or present. Example, L. Albacutya—Fig. 5.

3, typical clay or gypseous clay lunette, asymmetric profile with steep windward slope. Example, L. Wandella—Fig. 3A.

Note that role of salts in evolution of basins and associated dunes becomes more effective from type 1, low salinity, beach controlled dune to saline groundwater control of processes and products in type 3.

mine if a crescentic lake-shore dune is composed of clay, sand, gypsum or a mixture of all three. In some lakes, the cross-sectional asymmetry is clear enough to provide immediate indications of high clay content. It is equally true that some quartz dunes are identifiable by reason of irregular blowouts on the downwind margin (cf Figs 3A, B, 7).

In some cases, it is not possible from aerial photography or topo-profiles to estimate composition; all are lunette in plan and therefore constitute a group of lakeshore transverse aeolian forms. Moreover, in some areas both quartz- and clay-rich dunes occur in proximity to or in combination with each other.

In those instances where the lunettes possess all the characteristics described by Hills, such as at Kerang and Lake Cooper which are classical representatives of the original definition, the term always implies a clay-rich composition. But composition may range through a wide range of mineral associations from clay through gypseous to quartz-rich dunes with a variety of mixed components. Thus the sand-sized gypsum-rich lakeshore irregular dunes on the margin of Lake Frome with analogues in Lake Tyrrell are very different from the small irregular forms at Kerang. Both have formed under late glacial conditions about the same time and by similar processes but the resultant forms are very different. The variation results not only from different composition but also from a difference in scale. Thus the huge clay-rich dune complex of Chibnalwood (Willan-

dra Lakes) with irregular gullied form are morphologically more complex than those found on smaller lake basins (Dare-Edwards 1982). Bearing these factors in mind, it is both logical and consistent to apply an adjective to specify composition. Thus *lunette* denotes a transverse crescentic lakeshore dune the composition of which is specified by the appropriate term, clay or loam lunette, quartz sand lunette, gypsum lunette and so on.

An additional complication arises when we consider internal structure. Many lunette dunes when seen in cross-section, are composed of two units or texturally differentiated members. In gully sections at Albacutya (Fig. 6) quartz sands are often overlain by clay-rich sediments. Thus not only have there been different phases of lunette formation, but the sedimentary variations suggest different processes of dune construction on the same lake at different times. When these multiple units are involved, we may specify them as being *compound* types (cf Fig. 4B).

CLAY DUNES

TEXTURES AND STRUCTURES

The high clay content affects all aspects of clay lunettes including their topography, internal structure and origin; it presents a number of important questions: A, what physico-chemical conditions control their origins? B, are such environments represented in Australia today?

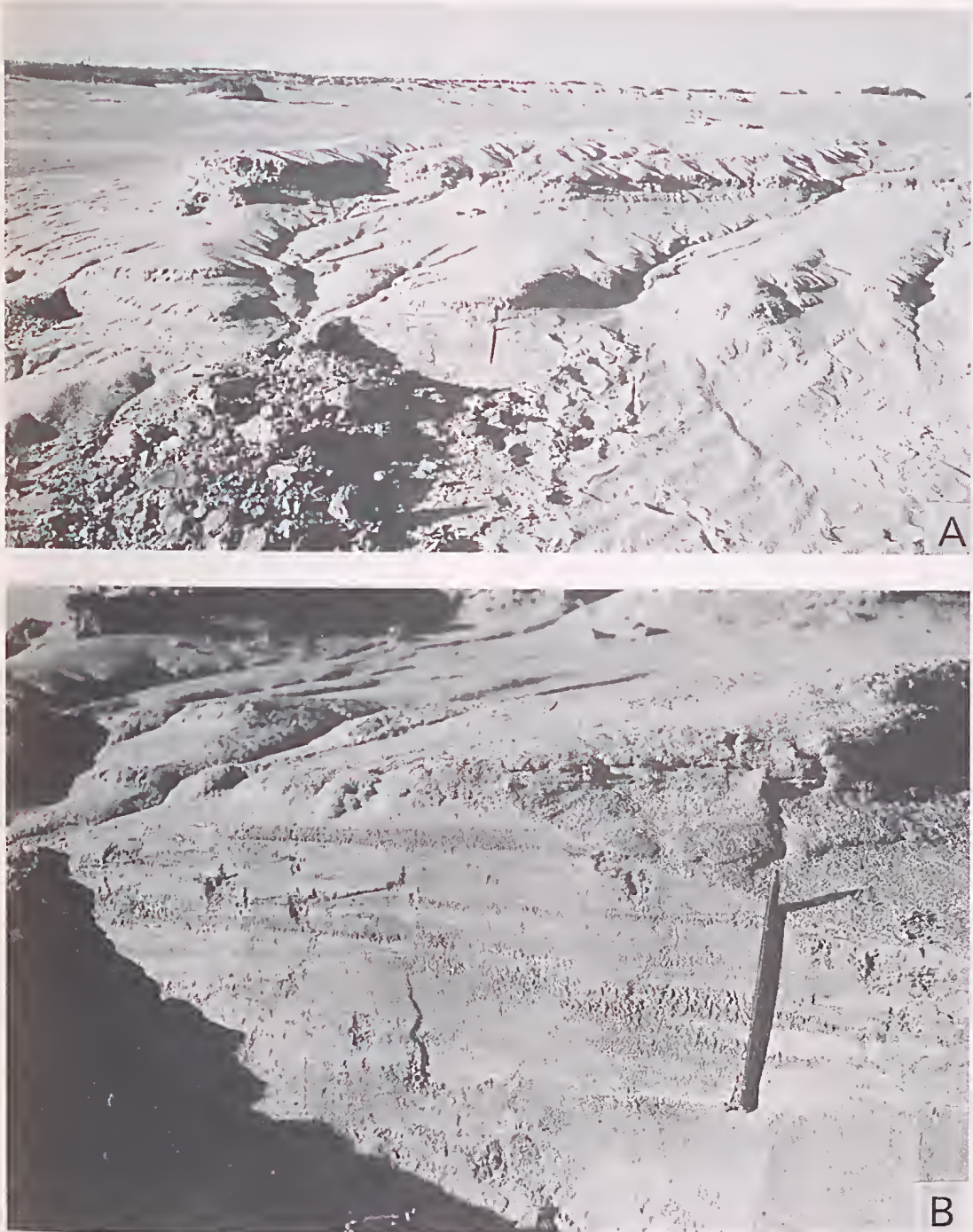


Fig. 8—Walls of China, Lake Mungo.

A, view north along southern margin of eroding lunette showing residual with planar bedding dipping at low angle towards lake floor on left.

B, Close up of central area of 8A. Alternate laminae of quartz-rich and clay-rich sediment have been deposited in a conformable sequence helping to produce the layer-by-layer succession characteristic of lunette growth (cf. Fig. 10, active clay dune in Texas).

The relevance of pelletal clay aggregates derived from drying mud on exposed lake floors first considered by Hills (1940, p. 4) was rejected because insufficient in-

formation was available to establish detailed similarity between the Texas clay dunes of Coffey (1909) and the Australian examples. The idea was revived later

(Stephens & Crocker 1946, Bettenay 1962) on the basis of Huffman and Price's (1949) description of clay pellets moving across tidal flats at Corpus Christi, Texas.

The first accurate Australian observation of clay pelletal aggregates with a description of their size and structure was made in an unpublished report by J. R. Sleeman of CSIRO (1973). He examined two samples in thin section, one from L. Cooper, the other from an undesignated lake near Kerang. Subsequently I have observed them in sections from all clay lunettes studied.

The clays occur in varying percentages of sub-rounded to elongated aggregates associated with quartz sands. Sorting and the size range of grains varies from bed to bed but within any particular layer, the size of clay pellets and associated quartz sands are similar, indicating that both have been subjected to identical sorting and transporting processes. The proportion of clay pellets to quartz grains varies considerably from dune to dune, and large variations may occur within a single dune. Thus in the Chibnalwood lunette the ratio of pelletal aggregate to quartz sand is approximately 4:1 (Dare-Edwards 1982) whereas through most of the Walls of China it is less than 1:1. But within a single dune such as the Walls of China or the L. Albacutya lunette, large variations in the clay pellet to sand ratio may extend from approximately 5:1 to 0.2:1. These changes in turn are reflected in textural analyses and result in bedding differentiation. Clay aggregates sometimes enclose silt and fine sand-sized quartz and carbonate crystals, although the percentage of silt (62 to 4 microns) is invariably small.

Thin-sections demonstrate the effective sorting of the primary sediment, a feature which is not apparent in the deflocculated samples. These instead, show strong bimodal peaks, one in the sand range near 0.2 mm, the other in the clay range.

The textural variation within the dunes also controls the type of sedimentary structures developed. Thus bedding is often diffuse being defined by alternate bands varying slightly in clay content, while finely laminated low angle bedding is often preserved below the solum, especially in sandier zones. For example, the fine laminae characteristic of the major part of the Zanci unit on the Walls of China (Fig. 8) when examined in section consists of well sorted sands and clayey sands with each lamina having a modal diameter reflecting a sedimentary population distinct from that of its neighbour.

The presence of texturally different layers, each with its own uniform population characteristics, demonstrates a mode of origin for the clay dunes different from that of quartz dunes. The growth of sand dunes by saltation transport up gentle windward slopes and the development of steep leeward sand-slip faces is well known. The downwind migration of the dune or lateral shifting of the crest results in successive erosion and deposition alternately truncating bedding and burying earlier deposits, a process which results in the cross-bedding normally associated with aeolian sediments. In the clay dunes, however, both the steep sand-slip faces

and truncation of bedding planes are normally absent (Fig. 8). Once deposited, each gently dipping layer must have remained stable during later depositional episodes. When seen in cross-section, bedding conforms to the topography of the dune reflecting successive stages in dune growth, with each bed superimposed uniformly over the last. Mobile dune forms were apparently not developed.

In the sequential generation of a clay lunette of the Wandella type the maintenance of constant low angle bedding combined with upward growth is associated with downwind migration of the dune crest (Fig. 9). Thus, where successive aeolian stratigraphic units are superimposed over each other as at Lake Mungo, the older units often outcrop or occur at shallow depth on the lakeward margin (Fig. 8).

DISTRIBUTION OF SALTS

Clay lunettes usually contain carbonate except those where deep pedogenesis has affected its removal from one level, concentrating it lower in the profile (Fig. 6). Gypsum is the only other soluble salt frequently observed in crystalline form; its occurrence is variable through the region. It is more common in clay dunes with a high clay content such as the Albacutya lunette than in the more sandy textured dunes where it may be absent as at Kanyapella.

Chlorides which originally would have accompanied clays derived from the saline lakes are not retained in crystalline form, although soils down-wind from lunettes often have high chloride contents (Macumber 1968, 1970) while the lunette clays retain high chloride exchange capacities (Dare-Edwards 1979). The highly soluble chloride, has been mainly leached from the dunes soon after deposition.

MOLLUSCA

The lacustrine faunas, especially the mollusca, provide additional evidence of sedimentary facies and depositional environments. They often occur in the lunettes where they were transported by wind action or, in the case of edible mussels, by man.

As early as 1836 the distinction between fresh-water and salt-water faunas was recognised. On the shores of an undesignated dry lake near Kerang, Mitchell (1839, p. 147) recognised overgrown aboriginal middens consisting of mussel shells collected from the lake. Later at Mitre Lake near the Grampians, he identified shells, which were almost certainly the inland water gasteropod *Coxiella*.

In the mollusca from the lunettes of the Willandra Lakes (Table 1) two principal assemblages are present each of which represent different salinity conditions. The unionids represented by the large *Velesunio ambiguus* represent the low salinity, fresh to brackish water environment, while *Coxiella* represents the high salinity facies.

TABLE 1

FAUNAL LIST FROM LUNETTES ON L. MUNGO, OUTER ARUMPO
AND L. CHIBNALWOOD

* <i>Vesunio ambiguus</i>	Large fresh to brackish water unionid
* <i>Lympaea tomentosa</i>	Sinistral coiled gasteropod
* <i>Bulinus (Isadorella) newcombi</i>	Planorbid dextral coiled gasteropod
* <i>Corbiculina</i> or <i>Sphaerium</i> sp.	Small lamellibranch
* <i>Pupoides (Themapupa) adelaidae</i> or <i>beltiana</i>	Small land snails
<i>Coxiella</i>	Small salt tolerant gasteropod

* Identifications by Dr Brian Smith, Museum of Victoria.

Within the same region, the occurrence of unionids and *Coxiella* are mutually exclusive. In the Willandra system the sediments representing the Outer Arumpo high water level phase contain unionids associated with ostracods. During the final phase of Zanci deposition equivalent to the building of the Chibnalwood lunette an important faunal transition occurred; unionids disappeared and were replaced by *Coxiella* (Bowler 1971). An identical situation occurs in L. Albacutya where unionids occur in quartz sand in the core of the inner lunette corresponding to the low salinity, beach-derived facies; this is overlain by the gypseous clay blanket with *Coxiella* (Fig. 6). The faunal assemblage again corresponds to the change in the sedimentary facies.

MODERN ANALOGUES

As stated earlier, the clay lunettes of southeastern

Australia represent fossil landforms, the legacy of earlier hydrologic events. Whilst small local occurrences of active deflation are known (Currey 1964, Macumber 1970) until recently, detailed observations of processes operating on the larger scale analogous to clay dune building were confined to examples outside Australia, notably Texas and North Africa. We now have from within eastern Australian inland basins, several documented examples of clay deflation sites, one from Lake Tyrrell, the other from the floor of Lake Eyre. Before considering these we should consider the Australian fossil forms in the context of examples described from other countries.

The first recorded and best documented of the modern examples are those of the Gulf of Mexico described initially by Coffey (1909) and subsequently studied in detail by Price (1948, 1963). Comparing morphology, textures and structures of Australian fossil forms and modern Texan examples (Figs 8, 10) confirms beyond doubt that the processes of formation are essentially the same in both regions (Bowler 1973).

The process described by Price and his co-workers has been outlined as follows (Price 1963, p. 767): 1, bare saline flats in dry regions crust over after prolonged insolation and wind action, the crust breaking down into aggregates of aeolian fineness, with sand-sized aggregates prominent in the debris. The aeolian aggregates are blown to leeward and form accumulations much like those formed where individual grains are sand size (Fig. 10). 2, the drying crust has been described as breaking down by three different methods: a, through the efflorescent growth of fine-grained, closely-spaced crystals of evaporite salts penetrating the upper layer of the crust; b, by the development in the upper layer of the crust of a microrelief pattern of domal blisters which break down with further drying; c, by the curling up of the thin

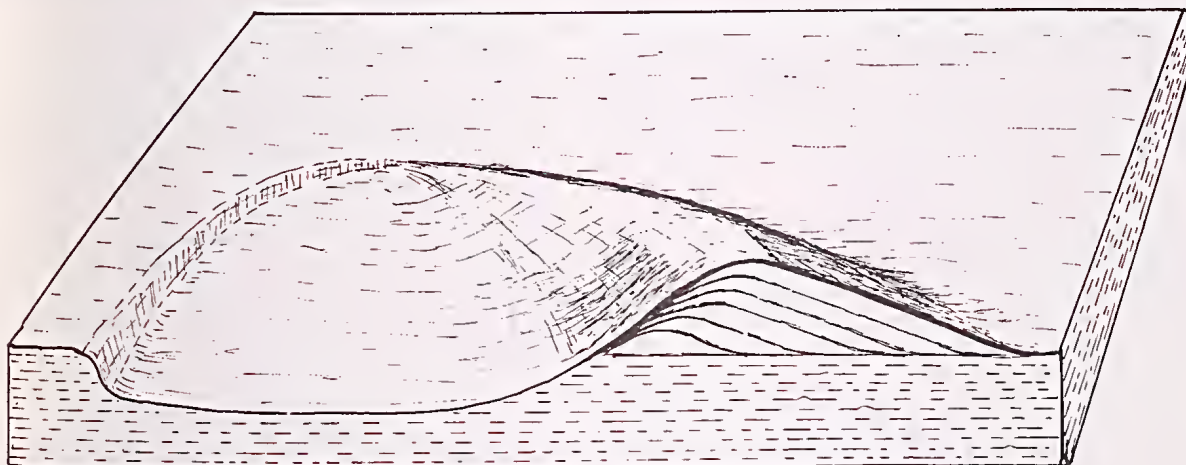


Fig. 9—Block diagram to illustrate morphologic features and growth stages of a typical clay lunette as evidenced from internal structures. Note that with preservation of low angle bedding, upward growth involves crestal migration away from lake source. Fossil cliff, characteristically present on upwind basin margin provides evidence of former (or present) groundwater outcrop zone producing active recession at toe of slope.



Fig. 10—Laguna Madre, Texas, 1969. View south towards lagoonal salt flat showing clay dunes accreting in the lee side of paling fence. Note planar laminae (cf. Fig. 8B) and polygonal crust developed on surface effectively preventing pellet migration between seasonal deflation episodes.

fragile surface layer of sun-cracked polygon chips which are then broken down mechanically by being swept to leeward along the surface of the crust. Where a layer of algae has formed on the crust, it retards deflation and its desiccation produces papery fibres which move with the other crustal debris. As the disintegrating crustal debris is blown to leeward, the wind sorts out the sand-sized aggregates and accumulates them on the crust or on rising ground of the border where they may be arrested by vegetation, chiefly of a grassy nature.

These features find equivalent expression in the ancient dunes of southeastern Australia. In thin-section both modern and ancient forms consist of sand-sized pelletal aggregates confirming that the Australian aeolian clays were derived from salinised lake floor in exactly the same way as those forming today near Corpus Christi, Texas.

Secondly, in a small 'satellite' pan on the east side of Tyrrell which we have named 'Pup Lagoon' (Fig. 11), clay pellet deflation occurs seasonally under today's climate. This is controlled by a groundwater regime, slightly different from that of the main basin from which the pan is separated by an aeolian barrier. The floor of the deflation pan is located a mere 70 cm above the main basin; it is subject to seasonal flooding, followed by drying, fall in watertable, efflorescence of salts in prepara-

tion for seasonally strong winds to transport the pellets to the eastern margin (Figs 12, 13).

Once the pellets are transported to the leeward margin they are trapped by vegetation and effectively stabilised by the hygroscopic action of enclosed salts, particularly halite, when temperatures fall and humidity nears dew point.

The deflationary process results here from the adventitious isolation from the main basin and especially the 70 cm difference in mud-flat surfaces. This small but significant difference and its influence on the deflation processes highlight the hydrological sensitivity of clay dune building.

DEFLATION FROM LAKE TYRRELL FLOOR, JANUARY, 1983

An instructive example of modern clay deflation occurred at Lake Tyrrell on January 26th, 1983. That day coincided with the passage of a cool front through southeastern Australia following a period of high summer temperature often exceeding 38°C. Strong southwesterly winds associated with the frontal system were raising great clouds of brownish dust from the dry, eroding wheatfields. Such dust originated mainly as a result of cultivation and grazing. On the other hand, from the lake floor, an area spared from man's direct interference, grey billowing plumes swept eastwards with each strong gust of wind, a phenomenon not observed previously here outside the narrow confines of Pup Lagoon. On this occasion the long drought through the preceding year had ensured effective desiccation of the playa surface. Strangely, the floor of Pup Lagoon remained stable although extensive pellet movement was occurring around its marginal samphire zone.

A transect across the playa margin on the east side near Pup Lagoon delineates 5 zones on the basis of topography, vegetation and hydrologic conditions (Fig. 14). A marginal chenopod zone (zone A, Fig. 14) on gypseous grey clays forms the eastern ridge rising about 6-8 m above the playa floor, passing down via a steep slope to a basal zone of succulent samphire (zone B). This frequently possesses a soft surface of pelletal fluffy clays prepared by efflorescence from the watertable lying 1 to 1.5 m below. On this day in 1983 strong winds were raising dust clouds from this zone, removing sediment in suspension and piling sandy pellets into shrub-coppice dunes around the toe of the slope and extending well up onto the chenopod ridge. This removal of sediment from the toe of slope constitutes a most important process in controlling over-steepening and slope retreat with consequent erosion of the underlying lacustrine or, in this case, aeolian sediment.

At the lakeshore edge of the samphire zone, an area usually boggy and impassable to vehicles, the watertable remained near the surface in January producing a soft slushy zone despite the long period of desiccation (zone C). Its permanent saturation ensures the relative stability of this surface as far as deflation is concerned. It was observed to be arresting some pellets in transit across it so that it appears rather as a potential accretion rather than deflation zone.



Fig. 11—Geomorphic map of L. Tyrrell showing location of Pup Lagoon, site of modern clay dune accretion. Note multiple ridges on east representing ancient development of lunettes during periods of Pleistocene hydrologic change.



Fig. 12—Clay deflation site at Pup Lagoon on margin of Lake Tyrrell.

A, summer conditions showing active deflation from clay flat in middle distance under the influence of southwesterly winds, Jan. 27, 1978. B, winter conditions with footprints leading across gluey mudflat to a small excavation site dug during previous summer. C, wall of excavation when freshly dug. Desiccation cracks pass down through greyish brown clays becoming black and sulphide-rich near the watertable at 50 cm in floor of pit. Desiccation cracks provide pathways for capillary evaporative loss and facilitate efflorescence and pelletisation at the surface. D, floor of Pup Lagoon during following summer showing early stage in the preparation for deflation. Desiccation polygons are outlined by dark puffy zones of efflorescence and clay pellet generation. Winds later in the season reproduce conditions as in 12A.

The main site of deflation on the playa floor was restricted to a zone marginal to the very outer edge of

the salt crust (zone D). Where the crust was very thin (1-2 mm only) slight buckling along tee-pee pressure

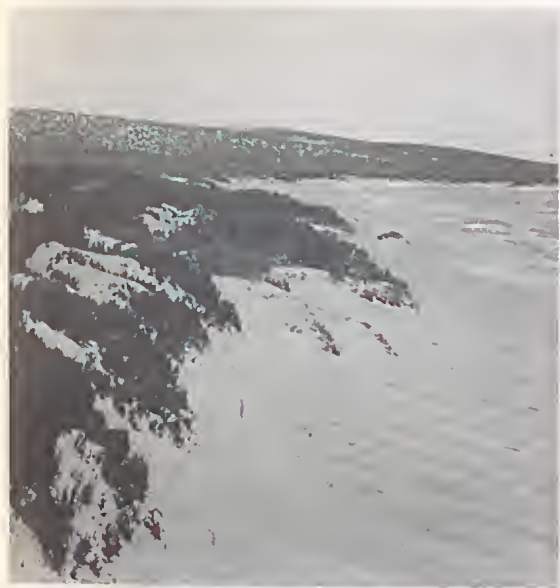


Fig. 13—Eastern margin of Pup Lagoon showing a rippled zone of clay pellets advancing eastwards to be trapped in dark samphire vegetation resulting in active clay dune growth to 1.5 m above clay flat. Skyline in background represents ancient lunette ridge built during the 36 000–16 000 BP dune building episode.

ridges was permitting strong winds to flip over and break up the salt flakes thus exposing the underlying clays to more intense drying (Fig. 15). A curious micro-hydrologic phenomenon existed here. Below undisturbed salt flakes, underlying clays were soft, slippery and water-saturated. By comparison, in those pelletal fluffy zones just a few centimetres to the east from which the crust had been removed by wind, the aerated zone to 5 cm and below seemed thoroughly dry. Apparently the salt layer, although very thin, is an effective inhibitor of evaporation loss. As soon as the crust is disturbed a completely new set of local conditions is initiated. Evaporative loss from the watertable (estimated to have been about 50 cm below) set up the interstitial salt efflorescence within the drying clays.

At Tyrrell on Jan. 26th, these processes produced a thin 1–2 cm layer of needle halite with crystal elongation perpendicular to the surface indicating upward growth. It was this phenomenon that was responsible for pushing up and breaking the surface clays. Driven by gusts of strong winds in excess of 30 km/hr, clouds of grey clay billowed off the lake surface while rippled ribbons of traction pellets streamed across the playa floor to be trapped in the marginal samphire producing an active clay dune ridge (Figs 13, 16).

These processes observed at Tyrrell and known to occur in almost identical fashion at Lake Eyre provide modern analogues of the climatic, hydrologic and micro-processes necessary to construct the larger, thick, lunette ridges of Late Pleistocene age. In so doing they provide excellent examples in helping to reconstruct those conditions that prevailed across southern

Australia during the windy summers of some 16 000 to 36 000 years ago.

In both the Texan and Tyrrell examples (Fig. 16), the advent of rain or onset of high humidity and low temperatures results in the formation of a surface crust 2–4 mm thick cemented mainly by halite, and sealing the active layer (Fig. 10). Within this crustal film clay pellets coalesce forming a stable protective envelope around free-flowing aggregates. Thus after the short seasonal dune growth the thin pelletal layer is permanently stabilised during the following humid season. In this way maximum progradation occurs in the inner dune slope. Pellets rarely form thick mobile accumulations; the steep sandlip faces of such accumulations have been recorded only during long droughts and periods of exceptional aeolian activity (Price 1963, p. 773).

In a recent field exercise at Lake Eyre, Mr. John Magee of the Department of Biogeography and Geomorphology established the presence of a broad zone of soft fluffy pelletal clays which under the influence of strong winds, is subject to active deflation (Fig. 17). This zone, apparently operating under the same processes described from Texas and Pup Lagoon, provides an example of extensive clay deflation from an inland salina, the actual extent and regional importance of which has yet to be identified.

SALTS

The role of salts in the clay pellet formation has been discussed by Price and Kornicker, (1961, p. 247) who recognise 'two phases of deflation in the flats'. In the first 'mudcrack polygon laminae break down when separated from the flat by wind as the particles are transported to the shore'. In the second phase, salt efflorescence breaks down clay into sand-sized pellets 'of quartzitic sand and silt in an envelope or with a matrix of lutitic sediment', a description which almost precisely corresponds to the fabric preserved within the Australian lunette sediments described above. Analyses of the mobile efflorescent layer from Tyrrell sites and Lake Eyre are set out in Table 2.

At L. Eyre and the floor of L. Tyrrell salts in the mobile pelletal layer are dominated by halite and gypsum while on Pup Lagoon the more soluble thenardite plays an important role. Previously gypsum crystallisation was thought to be the active component in clay pelletisation since, in the clay lunettes, it is almost always present. However, the gypsum being the 'millet seed' or discoidal variety is now known to have crystallised interstitially from groundwater during an earlier phase of the drying cycle before the efflorescence of the more soluble chloride and sodium sulphate. Indeed it is these more soluble components and especially halite which provide the active agents that prepare the clay surface for deflation as the analyses in Table 2 confirm.

OTHER FACTORS

Macumber (1970) questioned the need for surface water to be present in the initial stages of lunette formation. His evidence is drawn from topographically low

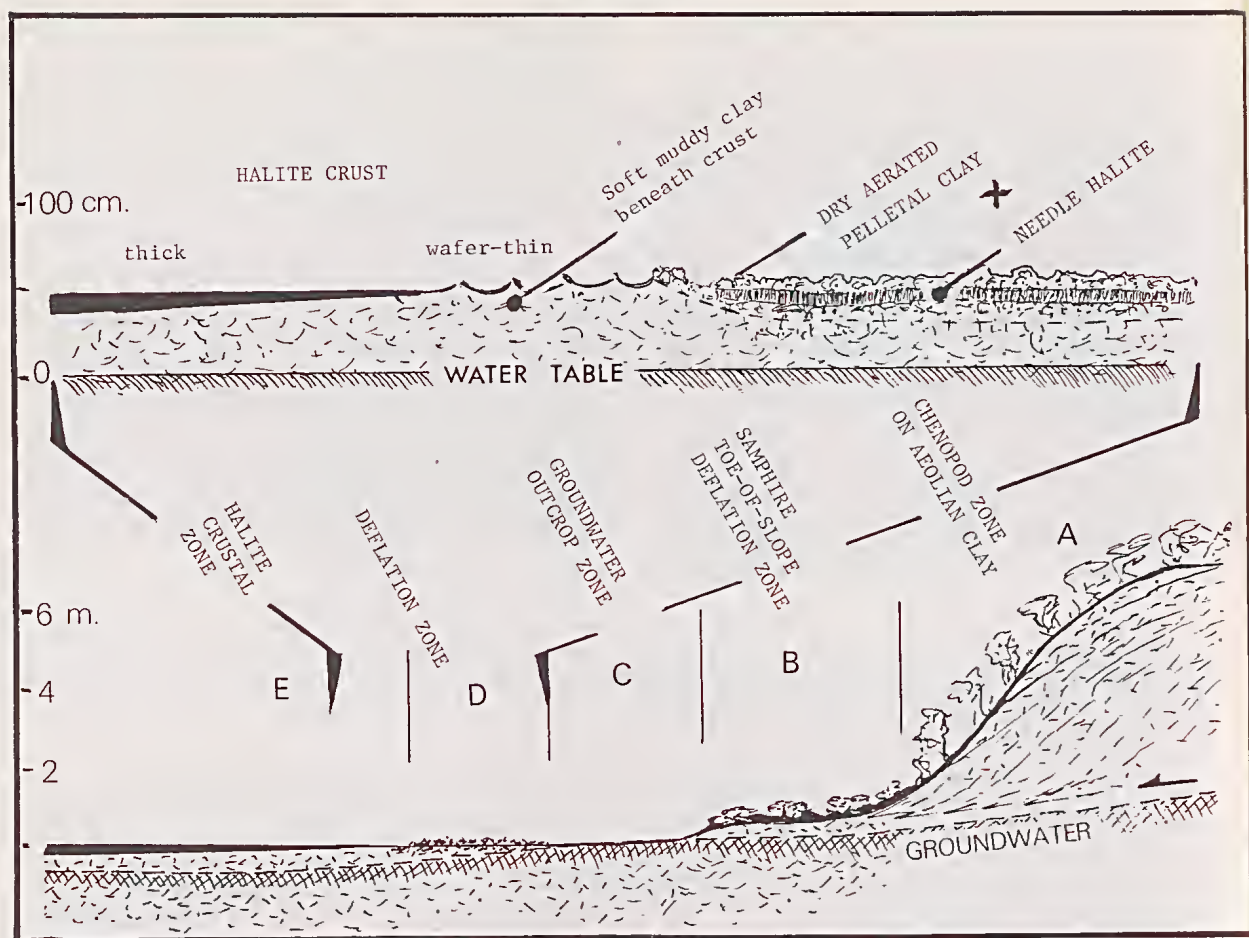


Fig. 14—West to east section across the eastern margin of L. Tyrrell showing relationship between topography, groundwater, halite crust and two active deflation zones: zone B at toe of main slope and zone D at edge of halite crust of playa floor. Width of zone D when active deflation observed on 26 Jan. 1983, ranged from less than 1 m to more than several hundred metres. Note development of vertically elongate needle halite, the active ingredient responsible for producing clay pelletisation in areas from which the salt crust was absent or broken up by wind.

and almost indiscernible ridges in the Kerang area which have developed by erosion of adjacent salt-affected areas. Macumber envisages vegetation destruction and breakdown in soil structure due to salinisation which may occur in low-lying areas after local or regionally controlled changes in watertables. Soil thus affected becomes liable to wind erosion which transports clay aggregates into the vegetated margin of the salt-affected area. This realistic explanation of such features must be taken into account in explaining the initiation of deflation basins.

In the Texas environment, the main aeolian transport of clays occurs between the months of March and November (Huffman & Price 1949, p. 120) in warm to hot seasons when strong insolation corresponds to steady onshore winds (Price & Kornicker 1961, p. 246). The summer months June, July, and August are characterised by strong winds from the southeast quadrant. In June with mean maximum air

temperatures of 28°C more than 50% of all winds blow from the southeast and more than 30% are greater than force 5. The coincidence of a strong, almost unidirectional wind regime and high summer insolation provides the conditions best suited for the drying of the flats, and formation of pelletal aggregates and transport into the northwestern lakeshore dunes. In southeastern Australia the surface is prepared by high evaporation rates following the winter wet season with the actual deflation process being restricted to periods of high wind velocity associated with the passage of frontal systems. Thus in the southeast at Lake Tyrrell, these are associated with both the northwesterlies that precede frontal systems and strong southwesterlies that often follow the passage of the front especially in summer. The process may continue until the onset of the next humid season usually in late autumn or winter. These conditions in the winter rainfall zone would almost certainly have prevailed during the Pleistocene production of major clay lunettes.

TABLE 2

CHEMICAL AND MINERALOGIC COMPOSITION OF MOBILE EFFLORESCENT ZONE CLAYS AND SALTS FROM LAKE EYRE, PUP LAGOON AT LAKE TYRRELL AND TYRRELL FLOOR.

Chemical data reported as weight per cent. Analyses by Jim Caldwell, Dept. Biogeography & Geomorphology, ANU.

MOBILE EFFLORESCENT LAYER

WET CHEMISTRY (needle halite layer, Fig. 10)	L. Eyre	Pup Lagoon	L. Tyrrell Floor
Total sulphate SO_4	6.25	10.5	1.57
Water-soluble SO_4	0.91	5.6	1.32
Insoluble sulphate (gypsum, by difference)	5.34	4.9	0.25
Total chloride Cl	15.26	0.24	29.14
Water-soluble CO_3	0.002	tr	NIL
Water-soluble HCO_3	0.039	0.024	NIL
Total carbonate CO_3	0.76	0.40	NIL
Organic C	0.26	N.A.	N.A.
1:5 pH	8.41	8.99	6.56
Na:K	190	35	
CALCULATED SALTS			
$\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$	9.57	8.80	0.44
Na_2SO_4	1.35	8.3	NIL
NaCl	25.16	0.40	47.0
$\text{Ca}(\text{M})\text{CO}_3$	1.20	0.29	NIL
NaHCO_3	0.05	0.22	NIL
MgSO_4	NIL	NIL	1.6

X-RAY DIFFRACTION

Gypsum	Gypsum	Halite
Thenardite	Quartz	Quartz
Halite	Thenardite	
Quartz	Disordered kaolin	Gypsum
Kaolin	Illite	Illite
Illite	Palygorskite (?)	Kaolinite
Palygorskite	Hi-Mg calcite	
Calcite	Halite	

Processes similar to those described here have been recorded by Boulaine (1956) in Algeria and by Coque (1962) in nearby Tunisia. In both cases they are related to inland basins controlled by saline groundwater regimes. In coastal west Africa, Tricart (1954) recorded the formation of small dunes (*bourrelets*) in estuarine environments of subtropical Mauritania and Senegal while more recently, Rhodes (1982) has described the seasonal mobilisation of pelletal clays on saline mud flats on the coastal fringe of the Gulf of Carpentaria. Thus the formation of clay dunes is not restricted to saline groundwaters of inland basins but may be active in many coastal regions.

An interesting clay dune occurrence has been recorded in the salinas of Patagonia by R. W. Galloway (*pers. comm.*) where seasonal aridity associated with saline groundwater produces pelletal aggregates which, in turn, are blown into lee-side dunes by very high

velocity westerly winds. The significance of this occurrence lies in the temperature regime of dune building; whereas all other examples recorded here lie in tropical or sub-tropical latitudes those in Patagonia are formed in cold high latitude arid conditions.

SOUTHERN AUSTRALIAN CLAY LUNETTES:
SUMMARY OF FORMATION

CHRONOLOGY

Substantial evidence indicates that the last period of major clay dune construction occurred in southeastern Australia about 17 000 B.P. (Bowler 1976, Sprigg 1979). Radiocarbon dates for this event represented by the Zanci Unit in the Willandra Lakes sequence, cluster between 17 500 and 16 000 B.P. in that region. Additional C 14 ages for lunettes at Albacutya, Lake Frome, Lake Corangamite, Lake Victoria (Gill 1971, 1973) and even in southwest of Western Australia point towards situations of regional extent permitting synchronous and large scale development of clay and gypseous clay dunes at this time. Although this corresponds to the last and most active period of clay dune building, earlier late glacial episodes are known. At Lake Mungo, the first clay dunes may have started as early as 30 000 B.P. but with intermittent deep-water conditions persisting until



Fig. 15 — L. Tyrrell floor, 26 Jan. 1983. Buckling zone with teepee structures in thin salt crust is broken by strong winds permitting drying and pelletisation of underlying clays. Note pellets drifting over crustal surface. Knife blades scale is 15 cm long.



Fig. 16—A, Laguna Madre, Texas, Sept. 1969. Shrub coppice clay mound accumulation on northern side of the tidal salt flat visible in background. Note crustal skin on mound and mud curls in depression developed after stabilisation by rain.
B, Lake Tyrrell, Jan. 1983. Rippled mounds of clay pellets accumulate in samphire vegetation under influence of southwesterly winds.

after 25 000 B.P. The controlling conditions may be determined by comparison with modern processes enabling us to reconstruct the hydrologic parameters that existed throughout the area during clay dune construction.

WATER AND SALTS

In the various theories of Australian lunette formation controversy centres on the presence or absence of water in the adjacent lake. The occurrence of modern clay dunes requires a particular combination of salinity and hydrologic regime, within which flooding plays an important part. In Texas, the clay flats remain bare and favourable to clay dune formation due to the periodic flooding by saline waters which prevent vegetation colonisation; on drying, efflorescence of salts assists in producing the clay aggregates. Flooding by sea water is similarly responsible for dune formation in the Casamance example (Vieillefon 1967) and on the West African Senegal delta region (Tricart 1954); in the Algerian example the seasonal inundation and the concentration of salt is ensured by high groundwater levels and by strong seasonality. In every example the presence of water is necessary to act as a vehicle to concentrate and distribute the salts.

The presence of salts, especially concentration of chloride, is necessary for two reasons. Firstly high salinities inhibit vegetation colonisation which would otherwise trap aeolian sediment on the dry lake floor. Secondly, the efflorescence of salts in the exposed clays provides one of the most important ways of producing sand-sized pelletal clay aggregates. This is the process which operates today on Lake Eyre, Lake Tyrrell, Pup Lagoon and on the margin of salinised depressions in the Kerang and Swan Hill districts during periods of summer drying and reduction in water level.

Tricart's comments (1954, p. 130), summarising the importance of saline waters in the deflationary evolution of *sebkhas*, apply equally well to their deflationary products in Africa as to clay lunettes in Australia. He emphasised the need for a continuous and relatively large supply of salts. In areas with high evaporation this can be ensured by a large seasonal inflow of fresh to brackish water from which the salt is concentrated during the dry season. Conversely, areas initially high in sulphates, carbonates, and chlorides are particularly favourable for the formation of *solanchaks*, which in turn are liable to erosion, dune formation and basin development.

During aeolian deposition chlorides are rapidly leached from the dune into the basin while carbonate and sulphate are retained in the aeolian sediment. The lunette-forming process and its associated hydrologic regime therefore represent a salt-separation environment as described by Boulaine (1954, p. 115). This helps preserve high chloride concentrations within the basin while calcite, dolomite and gypsum are preferentially removed.

As implied by Macumber (1970), the level and quality of groundwater relative to the basin floor are critical

for clay deflation. Today the seasonal rise and fall of approx. 70 cm below the floor of the mud flat at Pup Lagoon provides the driving mechanism enabling seasonal efflorescence from chloride saturated waters and pellet formation to occur. But as indicated earlier, this is a purely adventitious circumstance controlled by the slight difference in elevation between Pup Lagoon and the main basin floor which remains a groundwater outcrop zone throughout most of the year. Thus today, the conditions for regional and large scale dune building in southern Australia do not exist. This stands in marked contrast to conditions of late Pleistocene when numerous basins in southern Australia were actively producing such dunes. The explanation for these extraordinary conditions is twofold.

Firstly, the deflation and clay dune building conditions were preceded by a phase of regionally high watertables, the Mungo Lacustral Phase in southeastern Australia. In this period numerous basins which are now dry, were brim full of fresh water as their unionid faunas attest. This would certainly have resulted in regional watertables being much higher than today's. But with the change to a negative hydrologic budget that followed, surface waters diminished, lakes became saline and basins, previously fresh, were converted to groundwater discharge points. This reversal of the hydrologic balance corresponding to a major climatic change, produced conditions necessary for clay pellet formation and dune building.

Secondly, to enable the process to proceed in lakes such as Tyrrell or Frome where the watertable is at or near today's surface, the discharge budget must have been such that seasonal evaporation exceeded surface and groundwater discharge. This would produce the necessary drop in watertables to allow capillary rise, efflorescence and seasonal drying, a condition which at Frome and Tyrrell is not widespread today. This circumstance would be favoured by a slightly undulating basin floor in contrast to the billiard-table floors which now characterise these basins. Moreover, it was the change from high to low watertables which maintained the regional supply of salts to basins in which no salt supply is available today e.g., the numerous lakes near Hatfield or the Willandra Lakes unconnected to surface drainage.

ROLE OF WIND

In the earlier part of this essay I drew attention to the different disposition of quartz and clay components when both are present in the same locality. The maximum development of the quartz component occurs in the northeastern quadrant while the axis of symmetry of the clay dune has a more east to southeasterly orientation.

Two processes are involved in the orientation of quartz lunettes. The maximum development and orientation of lake beaches which provided the source of the dune sands is controlled by the complex interaction of winds, waves and littoral sediment transport in the lake. This, in turn, is reflected in the maximum development

of the quartz foredune. Evidence from modern lakes in the region suggests that maximum beach development occurs in the northeastern quadrant coinciding with the thickest dune sands as on L. Hindmarsh, L. Albacutya and L. Garnpung. In addition, the aeolian transport of quartz sand, although most active in summer, may have occurred at any time of the year provided the beach sands were dry and winds were of sufficient strength.

In the clay dunes, the annual duration of the dune building phase was restricted to a brief interval late in the dry season. Evaporation curves show that water-levels would be lowest, muds driest and conditions best suited for clay deflation at the end of summer or in early autumn.

Modern sand shifting winds ($F V^3$ where V is velocity greater than 9 knots) analysed from continuous anemometer records from Mildura airport produced the following seasonal resultants: summer 209°, autumn 242°, winter 273°, spring 248°. The summer resultant with its strong southerly component bears little resemblance to clay lunette orientation which is closer to the autumn or winter resultants. This is consistent with the formation of clay dunes in southern Australia being restricted to the February-April period. The combination of these factors (the construction of lake beaches, and the growth of quartz and clay dunes under different hydrologic conditions) has contributed to the asymmetrical disposition of the quartz and clay components in the lunettes.

LOCAL HYDROLOGIC VERSUS REGIONAL CLIMATIC INFLUENCE

In the examples of modern clay lunette formation discussed earlier, the controlling factors are dominantly local hydrology rather than regional climates. In Texas, flooding by sea water provides the triggering mechanism; in Algeria, saline groundwaters are involved in a particular tectonic setting while in Mauritania and Senegal a combination of fluvial and estuarine factors create the circumstances in which clay dunes form. The dunes are not controlled by climate alone.

The dominant influence of hydrologic factors other than climate is further evident in the distribution of the modern examples. On the Gulf of Mexico, clay dunes extend from the sub-humid zone near Corpus Christi south into the semi-arid regions of Mexico. Similarly in the Mauritanian-Senegal occurrences, precipitation increases rapidly southwards into the humid tropics but the clay dunes continue across the climatic gradient. This is reminiscent of a similar azonal distribution of the ancient Australian examples where lunettes of last glacial age occur from central Australia (Lake Eyre, Lake Frome region) through what are today semi-arid regions of the Murray Basin and the southwest of Western Australia and into the sub-humid and even humid regions of western Victoria and at Lake Omeo, in the southeastern highlands.

A striking feature of the Australian examples is that not only did hydrologically suitable conditions for lunette formation develop over a wide range of



Fig. 17—Footprints in soft rippled pelletal clays in active deflation zone at L. Eyre, October 1982. (Photo J. W. Magee)

physiographic and climatic settings but that these critical water balances should have appeared synchronously over such regions. This could only have been controlled by a major change in climate affecting the entire southern region of the continent in which lunettes that formed at that time remain as fossil remnants today.

The nature of the changes which controlled the synchronous development of glacial age lunettes involves a major contrast between the conditions that prevailed during the period of earlier regionally high lake levels and those that accompanied the drying of lakes and construction of dunes. In this respect it was largely the *direction* of change from regionally wet to regionally dry which made lunette building possible. By contrast, if we experienced a trend towards drier climates today, the landscape response would be quite different from that which characterised the expansion of dune building environments some 16 000-30 000 years ago.

In their history, the lake basins and associated dunes across southern Australia reflects a basic principle of geomorphology, viz. *the nature of the landscape response to any climatic or hydrologic change is determined as much by the pre-existing conditions as by the direction and nature of that change*. Thus the clay-rich and gypsum-rich lunettes of southern Australia represent the end products of a particular set of hydrologic parameters which were set up almost simultaneously over large regions in response to a major shift from regionally wet, high watertable conditions to dry windy environments coinciding closely with the maximum of the last global glaciation.

CONCLUSIONS

In Australia, relatively unaffected by glaciation, the imprint of Quaternary global climatic variations has long been poorly understood. The lunettes discussed here and the changes they represent provide a window into events of glacial age; in so doing they demonstrate

how this dry continent responded to late Quaternary global climatic rhythms.

As fossil features from the last glaciation, Australian clay lunettes find present day analogues in active clay dunes on coastal Texas, Senegal and the Gulf of Carpentaria while comparable inland playas are today forming clay dunes in Algeria, Patagonia and in certain parts of Australia. The controlling processes require a special combination of salt-affected surfaces subjected to regular flooding, followed by a seasonally dry climate to permit efflorescence and pelletisation of surface clays. Strong winds are then necessary to transport clay pellets and associated minerals, usually gypsum, to the vegetated playa margin.

The hygroscopic nature of associated salts plays an important part in the depositional behaviour of the clay pellet layers. As temperature falls and relative humidity increases to near dew point, salts associated with the last season's layer of pellets, hygroscopically absorb moisture; the layers become a sticky coalescing mass in which individual pellets adhere to each other so that on drying, a surface crust develops sufficient to stabilise and prevent any further movement. Thus next season's layer is deposited conformably over the last, building a layer-by-layer sequence characteristic of those lunettes where internal structures are preserved. By the nature of its conformable low angle bedding, as the dune grows in height, its axis of symmetry moves downwind thus maintaining its internal geometry.

The clay lunettes across southern Australia formed in response to a particular sequence of hydrologic events, the legacy of which is recorded on many lake basins over wide areas. This sequence began with a substantial wet phase, the Mungo Lacustral, in which many basins now dry were filled with fresh water. The widespread presence of surface water, even in regions now dry, identifies this as a period of major groundwater recharge. From evidence in the Willandra Lakes it appears to have lasted from at least 50 000 B.P. to near 36 000 B.P. marking it as a major period in the climatic evolution of Australian landforms. During this episode many quartz lunettes were formed from high water levels on northeastern lakeshore margins. It was this wet phase which set the scene for later dune building.

With a change from a positive to negative hydrologic budget around 36 000 B.P., surface waters contracted, lake levels fell and many basins were converted to groundwater discharge points. This period corresponded to an increase in salinity, deposition of large quantities of gypsum and eventually resulted in that critical balance of seasonal drying and flooding, the conditions necessary for pelletisation and clay lunette building. Although clay-dune growth proceeded episodically from about 36 000 B.P., the maximum and most widespread phase culminated between 18 000 and 16 000 B.P. signalling the expansion of dune building over large areas of the continent.

The changes recorded in lake basins in terms of salinities and hydrologic variations are no less remarkable than those events of comparable ages and

controlled by the same climatic rhythms in other continents. Thus the dramatic advance and retreat of ice sheets in Northern Hemisphere continents, North America or Europe, of the expansive deposition of loess blankets over huge areas of central China or western USSR, these all represent different responses to those same global rhythms that controlled the hydrologic changes and culminated in widespread dune building on the basins of southern Australia. Indeed in the wealth of stratigraphic, archaeologic and palaeoenvironmental information they have yielded over the past 15 years, the Australian lunettes continue to provide some of our richest records of Quaternary geological and human history.

ACKNOWLEDGEMENTS

Discussions with many persons have helped clarify the ideas presented here. These include, P. G. Macumber, C. R. Lawrence, R. J. Wasson, J. N. Jennings, A. J. Dare-Edwards and other colleagues. Mr. John Magee read and commented on the text.

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PROCEEDINGS
OF THE
ROYAL SOCIETY OF VICTORIA

Volume 95

NUMBER 4

ROYAL SOCIETY'S HALL
9 VICTORIA STREET, MELBOURNE 3000

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OBSERVATIONS ON THE ECOLOGY AND REPRODUCTION OF *SMINTHOPSIS LEUCOPUS* (MARSUPIALIA:DASYURIDAE)

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ABSTRACT: The results of trapping carried out over 5 years support the observations of others that *Sminthopsis leucopus* is found in a wide variety of habitats, and that capture rates are low. At Sandy Point Naval Reserve, Victoria *S. leucopus* was found in 2 vegetation associations (foredune complex and *Eucalyptus viminalis* woodland); it was most often captured in the foredune complex. Trapping success was never higher than 3.75%.

Field and laboratory studies on reproduction show that *S. leucopus* is a seasonally restricted breeder. Males survive beyond the time of birth of the young but breed in only one season. Females may breed in more than one season.

Within *Sminthopsis* fourteen species are recognised (Archer 1981, McKenzie & Archer 1982) but only four have been the subjects of studies on ecology and reproduction. At the time the study reported here was carried out observations had been made on reproduction in *S. crassicaudata* by Martin (1965), Ewer (1968), Godfrey (1969a), Smith and Godfrey (1970) and Godfrey and Crowcroft (1971), and in *S. macroura* (as *S. larapinta*) by Godfrey (1969b). Their findings have been summarised by Woolley (1973). More recently, observations on reproduction in *S. murina* have been made by Fox and Whitford (1982), and aspects of the ecology of 3 species studied. A comprehensive study of the ecology of *S. crassicaudata* has been carried out (Morton 1978 a, b, c) and observations made on the distribution and habitat of *S. leucopus* and *S. murina* (Morton *et al.* 1980) and habitat requirements of *S. murina* (Fox 1982). Some information on range length of *S. leucopus* has been obtained by Cheetham and Wallis (1981).

S. leucopus occurs in eastern New South Wales, southern and southeastern Victoria and Tasmania (Green 1972, King 1980, Morton *et al.* 1980). In Victoria the species has been recorded from a variety of habitats including sand dune complex, heath, woodland, open forest and semi-cleared areas (Land Conservation Council Reports 1972a, 1972b, 1973, 1974, 1976, 1980, 1982, Callinan & Gibson 1977). The vegetation in 17 habitats has been described; 15 by Morton *et al.* (1980); one, by Cheetham and Wallis (1981) and one by Menkhurst and Beardsell (1982). In New South Wales *S. leucopus* is found in heathland (King 1980) and in Tasmania, in diverse habitats which include coastal tea tree, dry sclerophyll forest and rain forest (Green 1972). The present distribution is restricted to within 150 km of the coast in southern Victoria and southeastern New South Wales (Morton *et al.* 1980); in Tasmania it is found in coastal areas and in the central highlands up to an altitude of 600 m (Green 1972). Although considered rare in Victoria (Frankenberg 1971) and Tasmania (Green 1972), Morton *et al.* (1980) suggest that the species may not be as uncommon as previously thought.

Little is known of its habits. In Tasmania, nests of either shredded bark or bark and leaves containing *S. leucopus* have been found in fire wood stacked in the bush and in the lining of an abandoned bus (Green 1972) and '45 feet up in the side of a gum tree' (Sharland 1962). Females with small young in the pouch have been captured in October (Green 1972, Cheetham & Wallis 1981).

An opportunity to study this little known species was provided by the finding of a population close to Melbourne in an area relatively free from disturbance. In 1968, 6 specimens were collected from the foredune area of the Sandy Point Naval Reserve, Mornington Peninsula, by the Victorian Fisheries and Wildlife Division, and in 1971 a further 2 specimens were collected in the same area by the Mammal Survey Group of the Victorian Field Naturalists Club (J. Seebeck pers. comm.).

The study was carried out from November 1971 to March 1975. Initially trapping was carried out to determine the preferred habitat of *S. leucopus* in the study area and to obtain specimens for a laboratory study of reproduction. In the course of this work it was found that several other small mammals, including *Antechinus stuartii*, *Rattus lutreolus* and *Mus musculus*, occurred in the study area. Later, the effectiveness of different types of traps was tested at the same time as a more thorough study was made of the habitat preferences of the small mammals in the study area. This was followed by a study of the distribution and home range of the small mammals in an area of the habitat preferred by *S. leucopus*. The trapping study is presented in a chronological sequence because methods changed in response to observations made in preceding years.

ECOLOGY OF *S. LEUCOPUS*

THE SANDY POINT STUDY AREA

The study area (Fig. 1A) lies in the sand dune region of the Sandy Point Naval Reserve. Four major vegetation associations, viz. the foredune complex, *Leptospermum laevigatum* scrub, *Eucalyptus viminalis* woodland and *Banksia integrifolia* woodland, occur within it. The

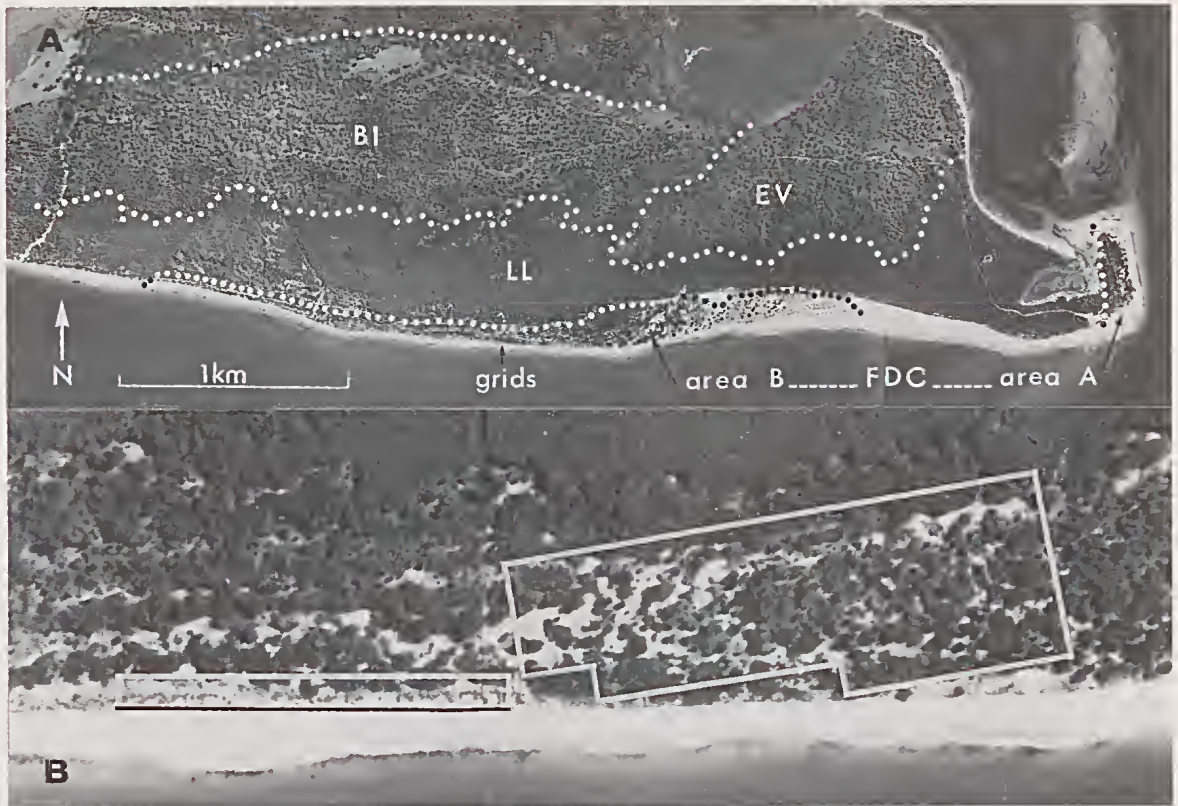


Fig. 1—A, aerial photograph of part of the Sandy Point Naval Reserve showing the boundaries of the four vegetation associations and the location of the trapping grids in the study area. FDC=foredune complex, LL=*Leptospermum laevigatum* scrub, EV=*Eucalyptus viminalis* woodland, B1=*Banksia integrifolia* woodland. B, the positions of the trapping grids in area B of the foredune complex. Small grid 100×20 m; large grid 280×100 m (north and east boundaries).

foredune complex, found in two areas (A and B), carries *Ammophila arenaria*-*Spinifex hirsutus* grassland on the seaward side. Moving inland this community is replaced by low shrubs of *Acacia sophorae* and *Leptospermum laevigatum*. Behind this is the dense *L. laevigatum* scrub. The boundaries of these vegetation associations are shown in Figure 1A, and the location of the trapping grids set up within area B of the foredune complex in Figure 1B. A description of the fire and clearing history, vegetation and soils of coastal sands in the reserve and details of the plant species occurring in each of the vegetation associations can be found in Robin and Parsons (1976).

TRAPPING NOVEMBER 1971-AUGUST 1972

Between November 1971 and August 1972 trapping was carried out in 3 of the 4 vegetation associations in the study area. Both large (23×8×9 cm) and small (16×5×6 cm) Sherman aluminium box traps and Tomahawk 1.25×2.5 cm mesh wire traps (40×13×13 cm) were used. The Sherman traps were baited with a mixture of peanut butter, bacon and walnuts and the wire traps with either the mixture or raw meat. Trapping was done in the months of November and

December 1971 and January, June, July and August 1972. In the first 3 months traps were set in the foredune complex (Area A), and in *L. laevigatum* scrub and *E. viminalis* woodland close to the vehicle track to the point, which can be seen in Fig. 1A; in the last 3 months they were set only in the foredune complex (areas A and B). Traps were not set in a regular line or grid pattern but in selected positions, about 10 m apart, which provided cover. In each trapping period the traps were set on the afternoon of the first day and checked and reset each morning for the following 3 or 4 days. The results of trapping in 1971 and 1972 are summarised in Table 1. *S. leucopus* was only captured in the foredune complex. Eight of the ten trapped were collected for study in the laboratory; all other mammals were released immediately at the site of capture. Trapping success, expressed as the number of individuals of a species caught per 100 trap-nights, was approximately 0.5% for *S. leucopus*. All species were captured in Sherman traps but the Tomahawk traps, because of the large mesh size, captured only *R. lutreolus*.

TRAPPING IN 1973

In 1973 the main object of trapping was to collect *S.*

TABLE 1
RESULTS OF TRAPPING IN 1971 AND 1972

Vegetation Association		No. trap-nights	No. each species trapped			
			<i>S.l.</i>	<i>A.s.</i>	<i>R.l.</i>	<i>M.m.</i>
Foredune complex	(A)	1027	(5)	7	20	148
	(B)	769	(5)	2	21	113
	(A + B)	1796	(10)	9	41	261
<i>L. laevigatum</i> scrub		180	0	1	0	4
<i>E. viminalis</i> woodland		333	0	18	11	4

S.l. = *Smintopsis leucopus*, *A.s.* = *A. stuartii*, *R.l.* = *Rattus lutreolus*, *M.m.* = *Mus musculus*.

The number of *S.l.* trapped (shown in brackets) represents individuals; the numbers of *A.s.*, *R.l.* and *M.m.* may include recaptures.

leucopus to study reproduction in this species. Because *S. leucopus* had previously been trapped only in the foredune complex most trapping was carried out in this vegetation association (areas A and B), but some was done in *E. viminalis* woodland and some in *B. integrifolia* woodland. Large and small Sherman traps were used. These were baited with a live cockroach, restrained by the spring wire on the back door of the trap, and a mixture of peanut butter, bacon and honey. The traps were set in selected positions as before. Trapping was carried out in 8 periods of from 3 to 8 days duration for a total of 39 days in the months of April, June, July, August, September, October and December.

The results of trapping in 1973 are summarised in Table 2. Fourteen of the 26 *S. leucopus* captured (including 3 found dead in the traps) were removed from the field. Others when first captured were marked by clipping digit 5 of the right pes. Only 4 *A. stuartii*, which were found dead in the traps, were removed from the field; the rest were toe-clipped as above and released. The *R. lutreolus* captured were released but not marked. All *M. musculus* trapped were killed to prevent them from excluding native species from the traps. As in 1971-72, *S. leucopus* was captured only in the foredune

complex. Again, there was a low overall trapping success (approximately 0.8%) for *S. leucopus* individuals, even though a different bait was used. The large and small Sherman traps were equally effective in the capture of *S. leucopus* (27 and 31 captures respectively), *A. stuartii* (48 and 50) and *M. musculus* (35 and 30). The larger *R. lutreolus* was mainly captured in the large Sherman traps.

Figure 2 shows the number of each of the four species captured each day in each trapping period, and the number of trap nights per period, in 1973. No obvious pattern in daily trapping success in relation to the total number of days the traps were set in each period can be seen for any of the four species, but changes in trapping success between trapping periods are evident. Trapping success for *M. musculus* was highest in the first trapping period (April) and the last (December). Although the reproductive condition of the *M. musculus* was not recorded it is known that populations of *Mus* in the South West Division of Western Australia have a distinct spring-summer breeding period during non-plague situations (Chapman 1981). Since all *M. musculus* trapped were removed from the field the increase in December may have been a result of recruitment from spring breeding. The lower number of

TABLE 2
RESULTS OF TRAPPING IN 1973

Vegetation Association		No. trap-nights	No. each species trapped			
			<i>S.l.</i>	<i>A.s.</i>	<i>R.l.</i>	<i>M.m.</i>
Foredune complex	(A)	75	0	2(2)	21	(7)
	(B)	3170	58(26)	94(22)	17	(56)
	(A + B)	3245	58(26)	96(24)	38	(63)
<i>E. viminalis</i> woodland		75	0	0	0	0
<i>B. integrifolia</i> woodland		75	0	2(2)	0	(2)

Abbreviation of species names as in Table 1. The numbers of *S.l.*, *A.s.* and *R.l.* include recaptures. The figures in brackets represent the number of individuals.

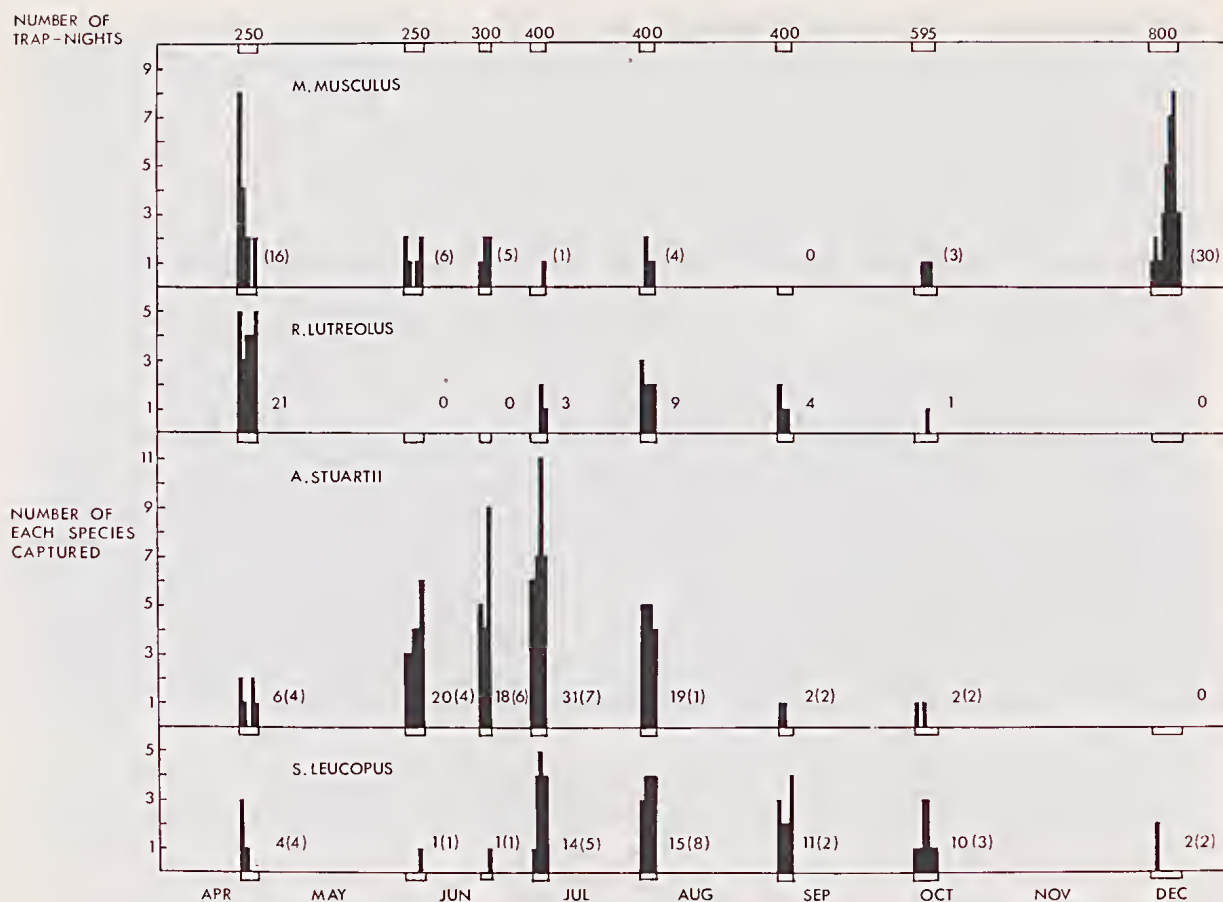


Fig. 2—The number of each species captured each day in each trapping period in 1973. The figures in brackets represent the number of individuals not previously captured. The number of trap nights in each trapping period is shown.

captures of *R. lutreolus* in each trapping period after April was probably the result of a deliberate attempt to avoid setting traps in areas in which *R. lutreolus* had been trapped, or in which their burrows were found. For *A. stuartii* trapping success for unmarked individuals was fairly constant (between 1.6% and 2.0%) from April to July but over this period trapping success calculated from the total number of captures increased from 2.4% to 7.25%. Trapping success fell in August and was very low in September and October. No animals were trapped in December when trapping effort was greatest. From April to August all *A. stuartii* trapped were males; only females (2 with pouch young) were trapped in September. This pattern of trapping success is consistent with that observed for other populations and the known life history of the species (Woolley 1966, Wood 1970). Trapping success for *S. leucopus* for both unmarked individuals (2.0%) and the total number of captures (3.75%) was greatest in August. Males were caught in all trapping periods but only 2 females were captured, one (in oestrus) in August and one (carrying pouch young) in October. These observations will be

further considered below in relation to the pattern of reproduction in this species.

TRAPPING IN 1974

Trap effectiveness and habitat preference study

Because overall trapping success for *S. leucopus* was low in previous years when Sherman traps were used, two specially designed live traps, an Elliott box trap and a funnel trap (Fig. 3) were tested in an attempt to find a more effective trap. The Elliott trap (26 × 10 × 10 cm) was slightly larger than the large Sherman trap. It had the same treadle mechanism as standard Elliott traps but the walls and roof were made of perforated aluminium (apertures 4 mm square). The funnel trap consisted of a plastic pipe 11 cm in diameter and 31 cm deep, sealed at the base, and with a polythene funnel held in place by a removable wire handle at the top. The funnel was 7 cm deep and the aperture at the base of the funnel 3.5 cm. This trap was designed to be hung in trees or shrubs; the base was perforated to provide drainage. The effectiveness of these two new traps was compared with large Sherman traps and break-back mouse traps, the latter

sometimes being considered to be more effective in sampling some species of small mammals than live traps (see, for example, Barnett *et al.* 1976, Fox & Posamentier 1976).

Trapping was carried out in the foredune complex (area A) between 11 and 15 April, in *L. laevigatum* scrub between 19 and 23 April, in *E. viminalis* woodland between 2 and 6 May, and in *B. integrifolia* woodland between 10 and 13 May. Fifty of each of the four types of traps, baited as in 1973, were used. One of each was set at 50 sites spaced 15 to 30 m apart in each of the vegetation associations. The traps were set for four consecutive nights, giving a total of 800 trap-nights in each vegetation association. The Sherman, Elliott and break-back traps were set close to each other on the ground and the funnel trap was suspended in vegetation up to 2 m above the ground.

All *S. leucopus*, *A. stuartii* and *R. lutreolus* captured alive were released at the point of capture after being individually numbered by toe-clipping. All *M. musculus* and the one *Rattus rattus* captured were removed from the field. One hundred and forty-one *M. musculus* and 1 *R. rattus*, as well as 15 *A. stuartii*, 1 *S. leucopus* and 3 *R. lutreolus* found dead in the traps were lodged in the Western Australian Museum. The results of trapping are shown in Table 3. *M. musculus* and *A. stuartii* were trapped in all vegetation associations; *R. lutreolus* in all but *L. laevigatum* scrub; *S. leucopus* in the foredune

complex and *E. viminalis* woodland, and the one *R. rattus* in the foredune complex. The numbers of individuals of each species captured in each vegetation association (Table 3) show that *M. musculus* was the species most commonly trapped (157 individuals), but fewer were trapped in *L. laevigatum* scrub than in the other 3 associations. The second most commonly trapped species was *A. stuartii* (40 individuals), the largest number being taken in *E. viminalis* woodland. The numbers of *R. lutreolus* (14 individuals), *R. rattus* (1 individual) and *S. leucopus* (3 individuals) were much lower, and none of these was taken in *L. laevigatum* scrub.

As in previous years, trapping success for *S. leucopus* was very low (0.5% in the foredune complex) even though a variety of live traps was used. Whether this reflects the rarity of the species or its trap shyness cannot be assessed, but it is in accord with the results of other workers (see Cheetham & Wallis 1981). Because trapping success was the same in 1974 as in 1971-72 it seems unlikely that the removal of 5 individuals from Area A at the earlier date had affected population levels. The 3 *S. leucopus* were captured in Sherman traps (Table 3). *A. stuartii* were captured in all four types of traps, the Sherman traps being the most effective. *R. lutreolus* and *M. musculus* were trapped in Sherman, Elliott and break-back traps. Sherman and Elliott traps were equally effective in capturing *R. lutreolus* but only

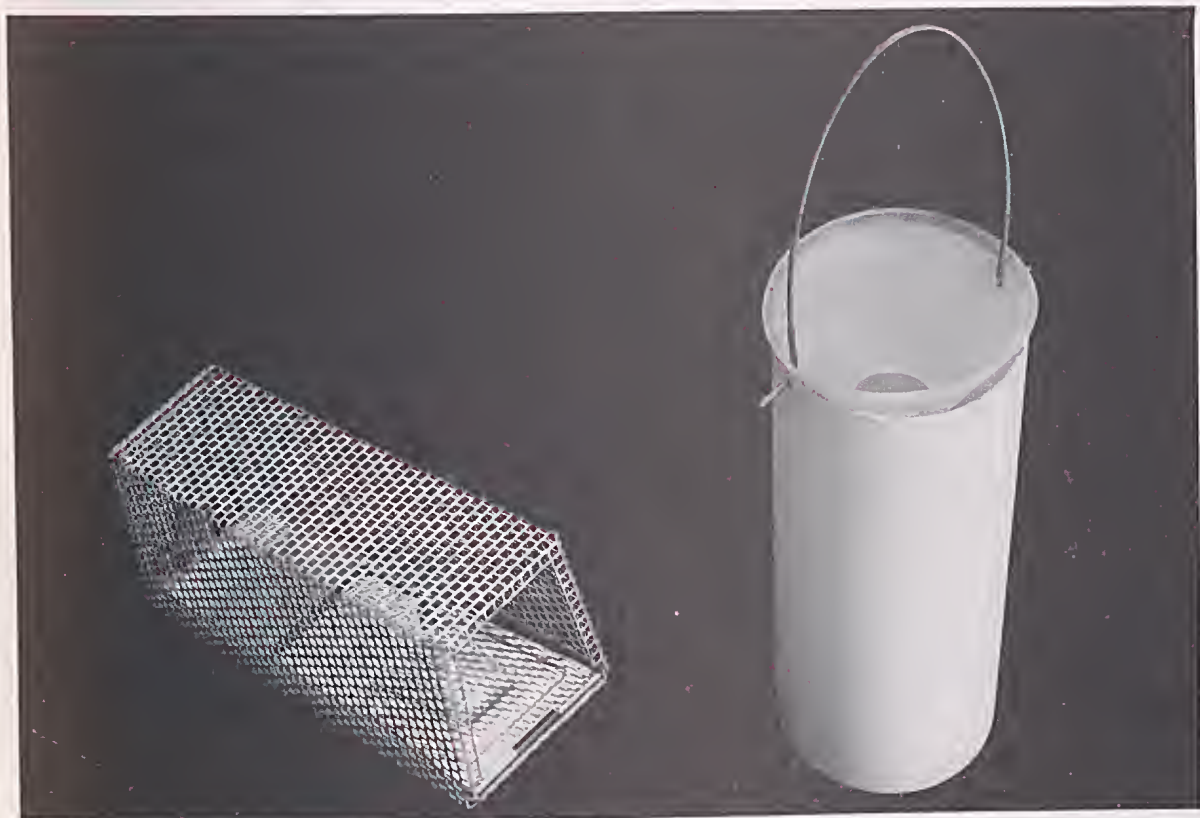


Fig. 3—The two specially designed live traps (Elliott box trap and funnel trap) used in 1974.

TABLE 3
RESULTS OF TRAPPING IN 1974 TO TEST TRAP EFFECTIVENESS AND HABITAT PREFERENCE

Vegetation Association	Type of trap	No each species trapped				
		<i>S.l.</i>	<i>A.s.</i>	<i>R.l.</i>	<i>R.r.</i>	<i>M.m.</i>
Foredune complex (A)	S	2	7	4	0	10
	E	0	5	6	1	26
	F	0	0	0	0	0
	B	0	0	0	0	22
	Total	2(2)	13(4)	10(5)	(1)	(58)
<i>L. laevigatum</i> scrub	S	0	11	0	0	4
	E	0	1	0	0	3
	F	0	1	0	0	0
	B	0	4	0	0	6
	Total	0	17(9)	0	0	(13)
<i>E. viminalis</i> woodland	S	1	15	3	0	11
	E	0	3	4	0	6
	F	0	0	0	0	0
	B	0	7	1	0	30
	Total	(1)	25(19)	8(6)	0	(47)
<i>B. integrifolia</i> woodland	S	0	7	5	0	6
	E	0	3	1	0	12
	F	0	0	0	0	0
	B	0	0	0	0	21
	Total	0	10(8)	6(3)	0	(39)

Trap types: S = Sherman, E = Elliott, F = Funnel and B = Break-back. Abbreviation of species names as in Table 1, plus *R.r.* = *Rattus rattus*. The total number of each species trapped includes recaptures. The figures in brackets represent the number of individuals.

one of this species was caught in a break-back trap. Most of the *M. musculus* were captured in break-back traps. The one *R. rattus* captured was in an Elliott trap. Only one animal (an *A. stuartii*) was captured in the funnel traps. Of the three types of live traps tested, Sherman traps were found to be the most effective for the capture of *S. leucopus* and *A. stuartii*, and as effective as Elliott traps for the capture of *R. lutreolus* and *M. musculus*.

The one *S. leucopus* trapped in *E. viminalis* woodland, which was found dead in the trap, was misidentified as *A. stuartii* until after the completion of trapping in 1974. Thus it appeared from the habitat preference study, and from the results of trapping in previous years, that *S. leucopus* was found only in the foredune complex. Because all species were thought to occur together only in the foredune complex the study of distribution and home range of the small mammals was carried out in that vegetation association, using Sherman traps.

Distribution and home range of the small mammals in the foredune complex

Part of area B of the foredune complex was selected

for this study (grids, Fig. 1A). In area B, the grassland does not extend along the length of the foredune complex, which in parts has been eroded by wave and wind action with the formation of cliffs up to 2 m high. The distance between high water mark and the *L. laevigatum* scrub varies from 20 to 90 m. To examine the distribution of mammals in the two major plant communities within the complex it was necessary to set the traps on two adjacent grids. One grid, with 20 trap sites, was in grassland and the other, with 80 trap sites, in the *Acacia-Leptospermum* community and edge of the *L. laevigatum* scrub. The positions and dimensions of the two grids are shown in Figure 1B. One hundred Sherman traps (50 large, 50 small) were used. One trap was located at each trap site and large and small traps were placed 20 m apart on alternate lines within the grids. The traps were baited as above and in all but one of the 11 trapping periods between June and October were set for 2 consecutive nights; in the seventh period they were set for one night only, giving a total of 2 100 trap-nights. They were inspected early each morning. Between trapping periods they were left closed and unbaited. Three species of mammals (*S. leucopus*, *A. stuartii* and *M. musculus*) were captured. All were individually

numbered by toe-clipping at first capture and released at the point of capture. The failure to capture *R. lutreolus* in this study suggests that the distribution of this species within the foredune complex is patchy and that the grids did not encompass the territory of any. Observations made on the reproductive condition of the *S. leucopus* will be considered below.

In the 11 trapping periods 31 *S. leucopus* (9 individuals—6 males, 3 females), 5 *A. stuartii* (2 individuals—1 male, 1 female) and 43 *M. musculus* (17 individuals) were captured. It can be seen that *S. leucopus* and *M. musculus* were trapped in both the grassland (small grid) and shrub communities (large grid) of the foredune complex but *M. musculus* was trapped most frequently in the grassland and *S. leucopus* in the shrubland (Fig. 4A). *S. leucopus* was also trapped on the edge of the *L. laevigatum* scrub (trap line 1-15), which was the only part of the grid on which *A. stuartii* was captured.

Some individuals were captured more than once during the study. The trap sites at which these individuals were captured are shown in Figure 4B for *S. leucopus* and in Figure 4C for *M. musculus*. Considerable overlap in the range of individuals can be seen. The maximum distance between sites of capture for an individual *S. leucopus* was 260 m, for *A. stuartii* 60 m, and for *M. musculus* 200 m. The maximum range length for *S. leucopus* was more than twice that recorded by Cheetham and Wallis (1981). Some individuals were captured at different trap sites on consecutive nights in one or more trapping periods and in these cases the distances between sites of capture were as follows: *S. leucopus* male 2 (20 m, 90 m), female 3 (20 m, 60 m), male 4 (80 m, 90 m) and *M. musculus* 6 (40 m), 14 (40 m). One *S. leucopus* (male 2) was recaptured within 1 hour of release 90 m from the site at which it was released. The longest periods between captures of individuals of the three species during the 18 weeks of the study were as follows: *S. leucopus* male 1 (11 weeks), female 3 (13 weeks); *A. stuartii* female 2 (6 weeks) and *M. musculus* 2 (16 weeks).

A trapping success of 0.4% for *S. leucopus* (individuals) on the grids suggests that the population density had not been greatly affected by the removal of 17 animals (14 in 1973 and 3 in 1972) from area B of the foredune complex.

TRAPPING IN MARCH 1975

Fifty large Sherman traps baited with bacon and peanut butter were set for 3 nights in the foredune complex (area B) with the object of collecting *S. leucopus* for study of their reproductive condition. Four *S. leucopus* (2 male, 2 female) and 9 *M. musculus* were captured.

REPRODUCTION

ANIMALS AND METHODS

Forty-nine *S. leucopus* (39 male, 10 female) were captured between November 1971 and March 1975. Observations on the reproductive condition of the ma-

jority of these animals were made in the field at the time of initial capture and at any subsequent recapture. The width of the scrotum of males was measured, the pouch area of females inspected, and an attempt made to obtain a urine sample which was examined for the presence of spermatozoa in males or epithelial cells, which are indicative of oestrus, in females. The animals were also weighed.

Fourteen (11 male, 3 female) of the 49 individuals captured were maintained in the laboratory. One of the females had 8 young (5 male, 3 female) in the pouch when trapped and these were reared in the laboratory. Another female, trapped at Boneo Swamp near Rosebud, Victoria in 1974 was also held, bringing the total number of animals maintained in the laboratory to 23 (16 male, 7 female). Eight were held for less than 6 months, 8 for between 6 and 12 months, and 7 for longer than 12 months, the maximum period for any individual being 16 months. With the exception of the female with young, which was housed in a wooden cage with a floor area of 1 m², they were housed in glass-fronted stainless steel cages with wire mesh backs and tops and detachable nest boxes, and fed a minced chicken meat mixture supplemented with insects (Woolley 1982). The observations made on animals at the time of capture (see above) were made at intervals of 1 to 2 weeks, or more frequently in the case of females once epithelial cells were detected in the urine, on animals maintained in the laboratory.

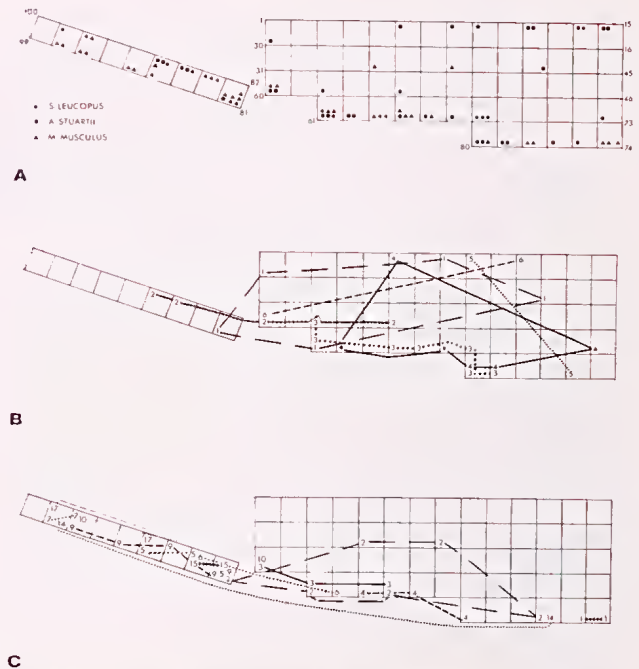


Fig. 4—A, sites of capture of *S. leucopus*, *A. stuartii* and *M. musculus* on the trapping grids in the foredune complex in 1974. B, sites of capture and range of individual *S. leucopus*. C, sites of capture and range of individual *M. musculus*.

Observations on the gross and histological appearance of the reproductive organs were made on 21 (15 male, 6 female) of these animals and on another 10 (6 male, 4 female) which were either found dead in the traps or were killed soon after capture. In males, the greatest width of the prostate (or membranous urethra in immature animals) was measured. One uterus of females in breeding condition was opened in saline and examined for the presence of eggs. Tissues for histological examination were fixed in Bouin's solution, stored in 70% alcohol, embedded in paraffin wax, sectioned at 8 or 10 μ m and stained with haematoxylin and eosin. Representative 10 μ m sections were prepared from one testis from each male. Ovaries were serially sectioned at 8 μ m and one diameter of Graafian follicles and of corpora lutea was calculated by counting the number of sections each appeared in and multiplying this number by 8.

RESULTS

Males: The same pattern of changes in body weight and scrotal width can be seen in laboratory reared and field animals, as well as in wild-caught males during their first

year in the laboratory (Fig. 5). Body weight is maximal in August and September and scrotal width in June, July and August. In these males spermatorrhoea commenced in June or July and continued in some until November. Four wild-caught males maintained in the laboratory into a second year could be distinguished by their greater body weight and scrotal width in the early months of the year. Two of these males, maintained until August, showed no recurrence of spermatorrhoea. With the exception of the two second year males prostatic thickening of the urethra was not evident until July (Fig. 5). In later months of the year all males had large prostates, which is illustrated by the width of the gland.

Histological examination of testes of males, other than those in their second year in the laboratory, revealed that spermatogenesis was occurring in all sampled in June and July, and in some as late as October. The seminiferous tubules were open and all cell types were present in the germinal epithelium. Spermatogenic activity had ceased in some males as early as August, and in others in September, October and December. The seminiferous tubules of these males contained only Sertoli cells; in some the tubules remained open, in others

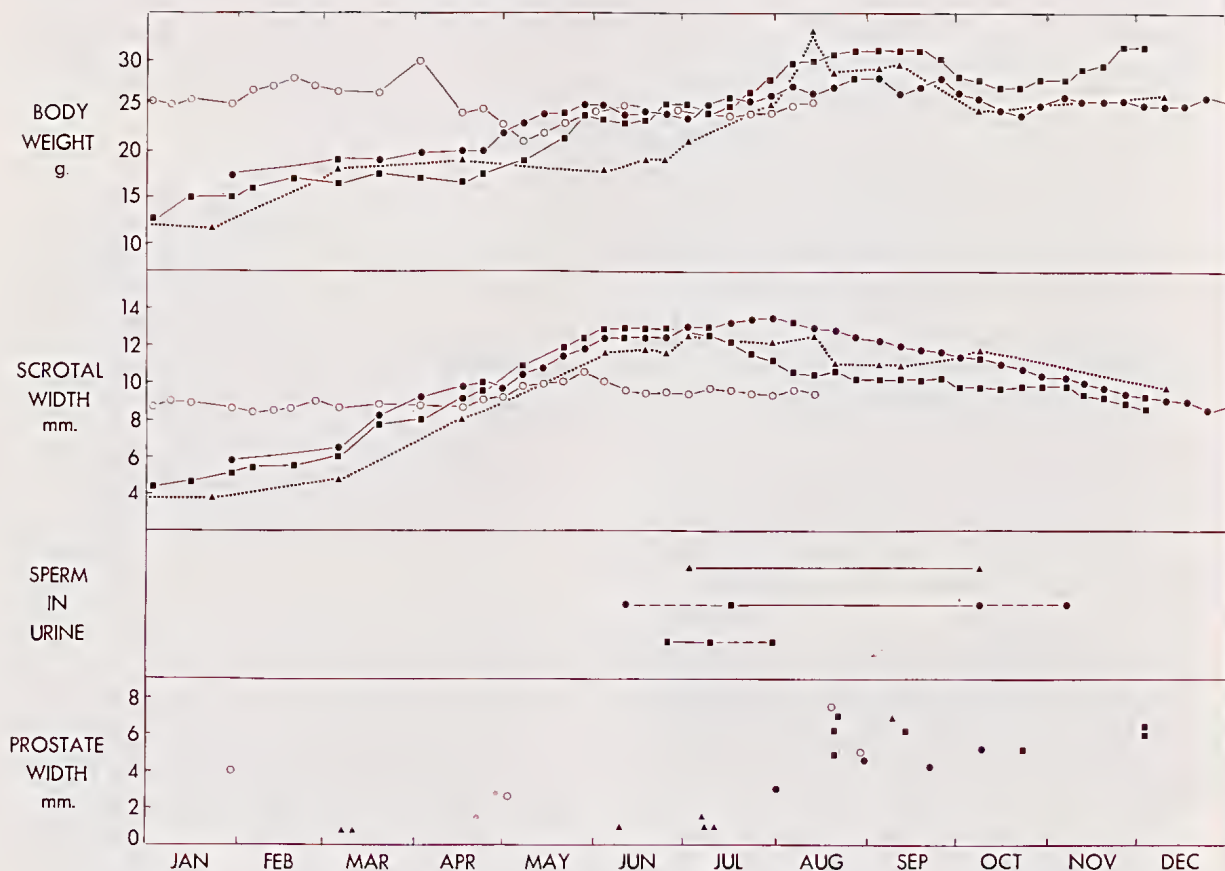


Fig. 5—Body weight and reproductive condition of male *S. leucopus*. The broken line (sperm in urine) indicates that not all individuals sampled were showing spermatorrhoea. Points represent the means for all animals examined (range 1 to 17). Δ field animals, \bullet laboratory colony—first breeding season, \circ laboratory colony—second breeding season, \blacksquare laboratory reared—first breeding season.

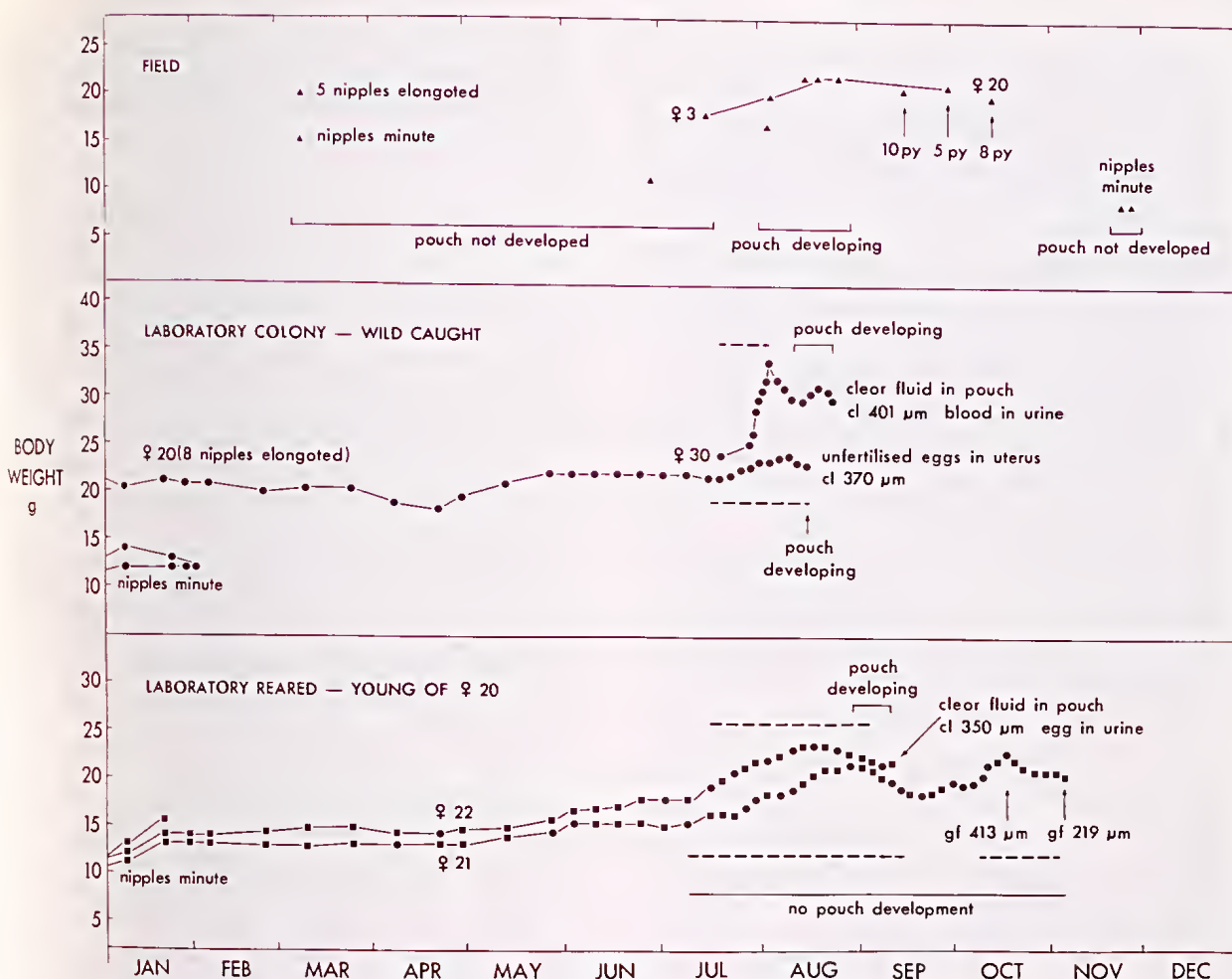


Fig. 6—Body weight and reproductive condition of female *S. leucopus*. Two field animals (one of which was recaptured several times and one of which was removed from the field) and four of those maintained in the laboratory are identified by number. Broken lines indicate the presence of epithelial cells in the urine of individual females.

they were closed. The seminiferous tubules of males sampled in March, that could be recognised as juveniles by their body weight and scrotal width, were closed and contained Sertoli cells, spermatogonia and a few spermatocytes. The seminiferous tubules of males in their second year, sampled in January, May and August, contained only Sertoli cells.

Females: *S. leucopus* has a Type 3 pouch (Woolley 1974) and all females examined had 10 nipples. The body weight and appearance of the pouch and nipples at capture of 10 females including one (female 3) which was recaptured several times is shown in Figure 6. Three females trapped in August were showing pouch development characteristic of pregnancy. One of these (female 3) and another 2 individuals were carrying young in the pouch when trapped in September and October. None of the 6 females trapped in March, June, July and November was carrying pouch young or showing pouch development. Of these only one, captured in March,

had elongated nipples characteristic of females that have previously suckled young.

Also shown in Figure 6 is the body weight and reproductive condition of 4 wild-caught and 3 laboratory reared females maintained in the laboratory. Epithelial cells first appeared in the urine of females in July. These oestrous females were housed with males but no matings were observed and no spermatozoa were detected in urine samples obtained from the females. Development of the pouch, preceded or accompanied by an increase in body weight, was seen in late August in 3 of the 4 females. Only an increase in body weight, was seen in the fourth. The reproductive organs of these females were examined to obtain further information on their reproductive condition. Two were killed when the appearance of clear fluid (milk) in the pouch signalled the end of pregnancy (or pseudopregnancy). In one of these females (30) there was blood in the urine and in the other (22), an undeveloped egg, both signs that 'parturition' had occurred. No eggs or embryos were found in

the enlarged uteri of these females, but both had large corpora lutea in the ovaries (14 in female 30, 11 in female 22). One female (20), killed before pouch development was maximal had unfertilised eggs in the uteri and 14 large corpora lutea in the ovaries. The one female (21) which did not show pouch development appeared to enter oestrus for a second time in October when epithelial cells appeared in the urine and body weight rose again. One ovary surgically removed from this female in mid-October contained 7 large Graafian follicles. When killed in early November, 7 degenerating Graafian follicles were found in the remaining ovary. There were no corpora lutea, and no eggs in the uteri.

An estimate of the gestation period in *S. leucopus* can be obtained from the observations made on female 30. In both unmated and mated females of other species (e.g. in *Antechinus stuartii*, Selwood 1980 and *S. macroura*, Woolley unpub.) a fall in body weight and a decline in epithelial cells in the urine has been correlated with ovulation. A second weight drop occurs in association with the onset of milk production and parturition (Woolley 1966, 1971). In *S. leucopus* female 30 the interval between disappearance of epithelial cells from the urine (and weight drop) and the secretion of milk (and a second weight drop) was 20 days.

The ovaries of 6 females, collected between January and early August were examined histologically. One obtained in January, one in February and two in March contained large numbers of small follicles with only a single layer of granulosa cells. One obtained in June contained follicles with up to 5 layers of granulosa cells and one in very early August, large follicles in which antrum formation had only just commenced. This female had epithelial cells in the urine, the rim of the pouch was slightly thickened and the nipples were red, indicating that she was in oestrus.

Except during the breeding period adult females (i.e. females that have reared young) can be distinguished from juveniles by their elongated nipples and by their greater body weight.

DEVELOPMENT OF THE YOUNG

Female 20, captured in mid-October with 8 pouch young (5 males, 3 females) estimated to be 3-4 weeks old, reared her litter in the laboratory. The young were weaned in late November, when the body weight (ca 9.0 g) of the females in the litter was comparable to that of 2 females captured in late November (see Figure 6) which were considered to be newly independent young. Males were up to 2 g heavier than females at weaning and their weight was comparable to that of a juvenile male captured in early December (not shown in Figure 5). One female young died in January; the other 7 young reached sexual maturity in July-August, at an age of about 11 months.

DISCUSSION

S. leucopus males appear to have only one short breeding season, commencing in late winter, in their

lifetime. Sperm production occurs from June to October but the prostate does not reach maximal size until August, which suggests that mating would not be successful before then. Thus the potential for breeding appears to be limited to a period of about 3 months. The absence of adult males from the trap returns in the early months of the year, together with the failure of males maintained in the laboratory for a second year to produce sperm, suggests that they do not normally survive to breed in a second year. However, their presence in the field for some time after the birth of the young shows that they do not experience the rapid 'die-off', in which all males die before the young are born, that occurs in some dasyurids that are seasonally restricted breeders (Lee *et al.* 1982). Lunney (1982) also has found that adult males are present in the population after the birth of the young. However, they had disappeared within a month of the young becoming independent.

Female *S. leucopus* were observed to enter oestrus in July and early August. Three females with pouch young were captured in September and October. These young were estimated, by comparison of their size with that of known age young of other species of *Sminthopsis*, to have been born in late August or September. In the laboratory, 'parturition' occurred in late August and early September. If gestation occupies about 3 weeks these observations suggest that mating occurs in August, at which time the males (see above) appear to reach breeding condition. In the field no evidence was found of breeding at other times of the year but in the laboratory one female, maintained beyond the time of expected birth entered oestrus for a second time. Although this female did not show pouch development characteristic of pregnancy, and therefore may have been abnormal, the possibility exists that females may undergo a second oestrus if unmated, or after premature loss of the first litter of the season. Whether or not this usually occurs could be simply determined by monitoring the reproductive condition of unmated females in the laboratory between July and November. Some advantage in the survival of males for several months after the onset of breeding, and beyond the time when births are known to occur, can be seen if the females are polyoestrous.

This analysis of the pattern of reproduction raises difficulties for the inclusion of *S. leucopus* in the group of species exhibiting the second of the life history strategies defined by Lee *et al.* (1982). Even if the females are found to be monoestrous, no males survive to breed in a second year, as they do in other species exhibiting this strategy.

ACKNOWLEDGEMENTS

We thank all the people who assisted with trapping, especially I. Robottom, G. Smith, J. Douglas, S. Webb, C. Ahern, R. How and W. Humphreys, and those in command at H.M.A.S. *Cerberus* over the period 1971-1975 for allowing us access to the Sandy Point Naval Reserve. S. Morton kindly donated one female *S.*

leucopus for the laboratory colony and R. Parsons made available aerial photographs of the study area. Permission to trap and collect animals was granted by the Victorian Fisheries and Wildlife Division. Financial assistance from the M. A. Ingram Trust in 1973 is gratefully acknowledged.

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Note added in proof

Observations by Read *et al.* (1982) on 1 female support the conclusion that *S. leucopus* may be polyoestrous. This female produced a single pouch young on 1st September. The young was removed and she returned to oestrus and mated on 29th September, 11 days after parturition. No young resulted from the mating and she returned to oestrus again on 28th October, but did not mate.

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TAXONOMIC STUDIES ON *SEPIOTEUTHIS* BLAINVILLE (Cephalopoda: Loliginidae) FROM THE AUSTRALIAN REGION

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ABSTRACT: *Sepioteuthis lessoniana* Lesson 1830 from Australia and *Sepioteuthis australis* Quoy & Gaimard 1832 from Australia and New Zealand are described and illustrated. A comparison is made between geographically isolated samples of each species, revealing morphologically distinct populations. *Sepioteuthis bilineata* (Quoy & Gaimard) is designated a *nomen dubium*.

Sepioteuthis was erected by Blainville (1823, p. 133) as the 'Calmars-seiches' to accommodate his new species *Loligo sepioidea*. Blainville's new group was defined as: 'Espèces dont le corps est ovale, déprimé, et dont la nageoire, fort étroite, s'étend de chaque côté, de l'extrémité antérieure à la postérieure: . . .'. The name, however, was adopted and latinised by Férussac (in d'Orbigny 1826, p. 154).

The genus was revised by Wülker (1913) and Adam (1937, 1939) and is known to occur in neritic tropical, subtropical and temperate waters worldwide, with the exception of the eastern Pacific and eastern Atlantic Oceans. Wülker included 20 species, 8 of which he considered insufficiently characterised; Adam synonymised a total of 25 names under four valid species. Those recognised by Adam (1939) are: *Sepioteuthis sepioidea* (Blainville 1823) from the east coast of Central America, particularly the Gulf of Mexico and the Caribbean Sea; *S. loliginiformis* (Rüppell & Leuckart 1828) from the Red Sea; *S. lessoniana* Lesson 1830 distributed from Hawaii to the Red Sea and from Japan to Australia; and *S. australis* Quoy & Gaimard 1832 from Australia and New Zealand.

Sasaki (1929) offered the following definition of the genus and although his work included only *S. lessoniana*, he significantly extended the original definition: 'Body conico-cylindrical, ending rather bluntly behind. Fins enormous, marginal; at maturity, extending the whole length of mantle; both together ovate. Hectocotylisation affecting the distal part of left ventral arm. Spermatheca present on the ventral part of buccal membrane, containing internally a pair of ramified seminal receptacles'.

Five species of *Sepioteuthis* have been reported from Australian and New Zealand waters: *Sepioteuthis lessoniana* (Gray 1849, Brazier 1892); *S. bilineata* (Quoy & Gaimard 1832, Hutton 1880, Kirk 1884, Dell 1952); *S. australis* (Quoy & Gaimard 1832, McCoy 1883, von Martens 1889, Whitelegge 1889, Brazier 1892, Hedley 1915, Berry 1918, Verco & Cotton 1928, Cotton & Godfrey 1940, Allan 1959); *S. mauritiana* (Brazier 1892, Meyer 1909), and *S. lunulata* (Brazier 1892). *Sepioteuthis lessoniana* has been reviewed in detail by Adam (1939). Gray's (1949) record from New Zealand is the only record from that country and may be regarded as doubtful (Dell 1952). Australian species are com-

pared with material from Indonesia and the Philippines in the present study.

Sepioteuthis bilineata (Quoy & Gaimard 1832) was poorly described from a single specimen from Western Port, Victoria, Australia, which was later lost (Quoy & Gaimard 1832, p. 68). Subsequent usage of the name applied only to the original description until Hutton (1880) introduced it into New Zealand literature for a specimen he had previously designated *S. major* (Hutton 1873). The name *S. bilineata* was adopted for the common species of *Sepioteuthis* in New Zealand by Kirk (1884), Suter (1913), Powell (1946, 1979) and Dell (1952). Adam (1939) suggested that *S. bilineata* was a *species dubium* but Dell (1952) considered it the senior synonym of *S. australis*, on the grounds that *S. bilineata* has page priority.

Sepioteuthis australis was well described and illustrated, also from a specimen from Western Port. It is found to be conspecific with material from New Zealand and the geographic variation within the species is discussed.

Sepioteuthis mauritiana and *S. lunulata* are both synonyms of *S. lessoniana* (Adam 1939, p. 30). However, Meyer's (1909) description of a specimen of *S. mauritiana* from Albany, southwestern Australia is considered by Adam (1939, p. 28) to be referable to *S. australis*.

MEASUREMENTS AND ABBREVIATIONS

Measurements (in millimetres) and abbreviations used in this paper are defined below. Indices unless otherwise specified are expressed as a percentage of dorsal mantle length and are denoted by the final initial I, e.g. $MW1 = MW/ML \times 100$. Beak measurements follow Clarke (1962) with the exception of baseline length (BL) and depth (D).

ML—	dorsal mantle length, measured from the anterior most point of the mantle to the posterior tip.
VML—	ventral mantle length, measured in the ventral mid line.
MW—	greatest mantle width.
HL—	head length, measured from the junction of the first pair of arms to the anterior end of the nuchal cartilage.

HW—	greatest head width, measured across the eyes.
FL—	greatest length of fins, measured in the mid line.
FW—	greatest width across both fins.
AL _{I, II, III, IV} —	arm length, of each right arm measured from the base of the first proximal sucker to tip of arm. (Arm I, dorsal; II, dorsal-lateral; III, ventro-lateral; IV, ventral).
HA—	hectocotylised arm length.
HC—	length of hectocotylus. Index expressed as a percentage of the hectocotylised arm length.
TL—	total length of tentacular stalk and club.
CL—	length of right tentacular club from the proximal most carpal sucker to the club tip.
AS _{I, II, III, IV} —	internal diameter of sucker rings of the largest sucker on each right arm.
CS—	internal diameter of the largest sucker ring on the right club.
GW—	greatest width of gladius.
RL—	length of free rachis, measured from anterior end of gladius to the point where the anterior edge of the vane joins the rachis.
RW—	width of rachis where it joins the vane.
SL—	spermatophore length, excluding cap thread.
SRI—	spermatophore sperm reservoir index, length of sperm reservoir as a percentage of the spermatophore length.
SWI—	spermatophore width index, greatest width of spermatophore as a percentage of the spermatophore length.
NL—	nidamental gland length.
ROL—	beak rostral length.
ROW—	beak rostral width.
WL—	beak wing length.
BL—	beak baseline length, measured in mid line between anterior tip of wing and posterior tip of lateral wall.
D—	beak depth, measured in vertical plane between rostral tip and end of wing.
HdL—	beak hood length.
CrL—	beak crest length.
LWL—	beak lateral wall length.

All measurements except suckers and beaks were made to the nearest 0.1 mm and rounded to the nearest millimetre. Sucker diameters and beaks were measured to the nearest 0.05 mm and rounded to the nearest 0.1 mm. The described specimens are housed in the collections of the Museum of Victoria, Melbourne (NMV), the National Museum of New Zealand, Wellington,

New Zealand (NMNZ), and the Zoologisk Museum, University of Copenhagen, Denmark (ZMC). Other repositories are indicated by WAM—Western Australian Museum, Perth, and MNHP—Muséum National d'Histoire Naturelle, Paris.

Regression analyses and comparisons between lines were done by the method given in Zar (1974, p. 228). Dates of publication of species described in Férussac and d'Orbigny (1835-48) are taken from Winckworth (1942).

Genus *Sepioteuthis* Blainville 1823

1828 *Chondrosepia* Rüppell & Leuckart, p. 21.

TYPE SPECIES: *Loligo sepioidea* Blainville 1823.

DIAGNOSIS: Body stout, slightly flattened dorsoventrally, tapers to a blunt point. Fins of adults and subadults large, muscular, extend for nearly the entire mantle length, continuous around posterior margin. Hectocotylisation affects distal portion of left ventral arm. Photophores lacking.

Sepioteuthis lessoniana Lesson 1830

Figs 1-4, 8a

1826 *Sepioteuthis lessoniana* Férussac in d'Orbigny, p. 155. (*nomen nudum*)

1830 *Sepioteuthis lessoniana* Lesson, p. 244, pl. 2.

1832 *Sepioteuthis guinensis* Quoy & Gaimard, p. 72, pl. 3, figs 1-7.

1832 *Sepioteuthis lunulata* Quoy & Gaimard, p. 74, pl. 3, figs 8-13.

1832 *Sepioteuthis mauritiana* Quoy & Gaimard, p. 76, pl. 4, figs 2-6.

1835 *Sepioteuthis dorensis* Férussac & d'Orbigny, *Sepioteuthis* pl. 3, fig. 2.

1848 *Sepioteuthis sinensis* Férussac & d'Orbigny, p. 304.

1852 *Sepioteuthis arctipinnis* Gould, p. 479, p. 49, fig. 593.

1881 *Sepioteuthis brevis* Owen, p. 137, pl. 26, fig. 1.

1884 *Sepioteuthis neoguinaica* Pfeffer, p. 4, pl. 1, fig. 2.

1896 *Sepioteuthis indica* Goodrich, p. 5, pl. 1, figs 9-19.

1898 *Sepioteuthis sieboldi* Joubin, p. 27.

1913 *Sepioteuthis malayana* Wülker, p. 478, fig. 7.

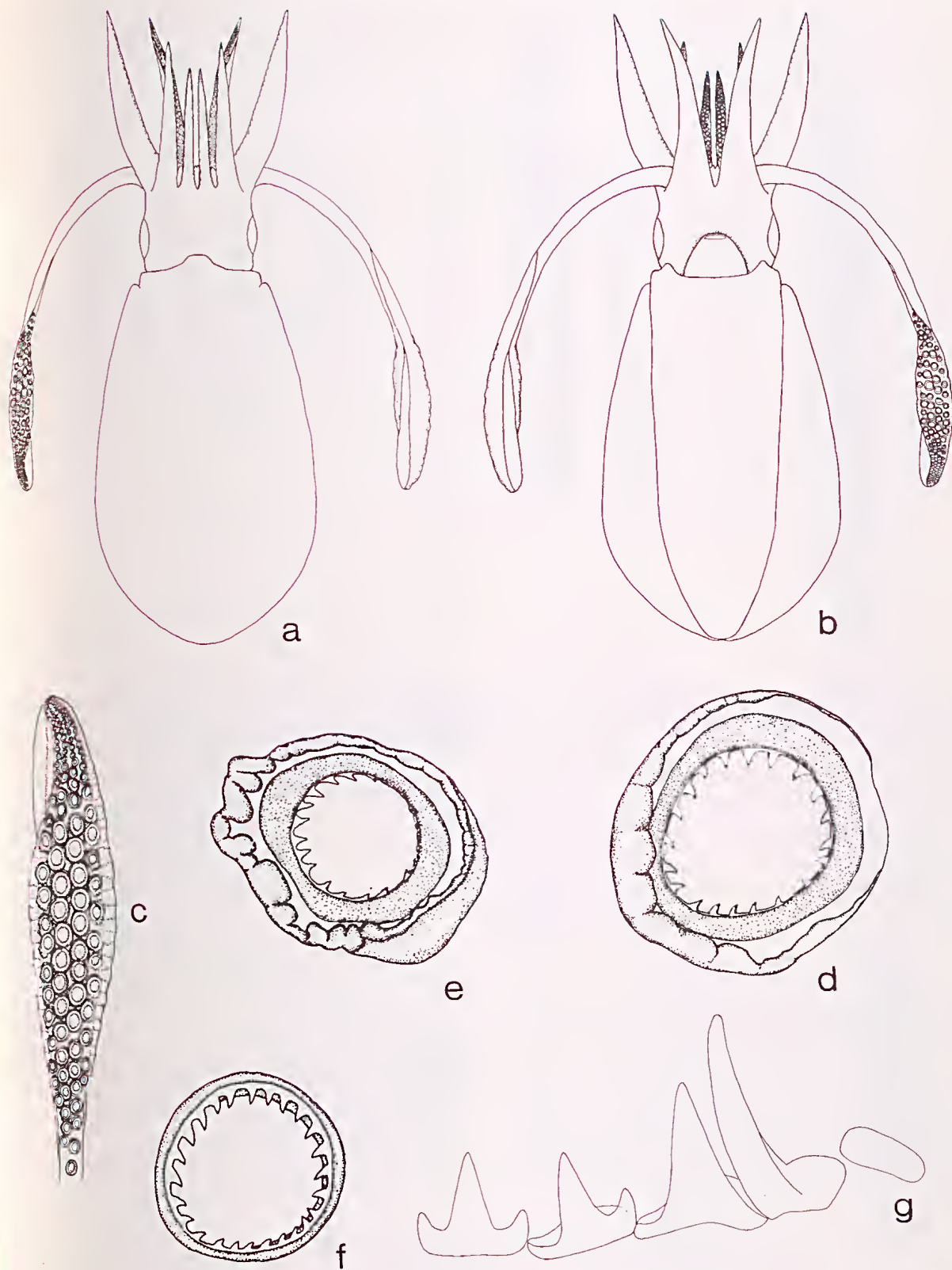
1928 *Sepioteuthis kremphi* Robson, p. 28, figs 13-16.

DIAGNOSIS: Fins widest in their posterior third. Buccal membrane well developed, suckers present on all lappets.

MATERIALS EXAMINED: See APPENDIX 5.

DESCRIPTION: *Mantle* stout (MW1 24-35), tapers to a blunt tip posteriorly; anterior dorsal lobe broad, rounded; ventrolateral lobes low, pointed. *Fins* large,

Fig. 1—*Sepioteuthis lessoniana* Lesson; male, NMVF31555, 155 mm ML. a, dorsal view. b, ventral view. c, left tentacle club. d, largest median manal sucker of club. e, largest marginal manal sucker of club. f, largest sucker ring from right third arm. g, radula. (d-f orientated distal aspect to top of page).



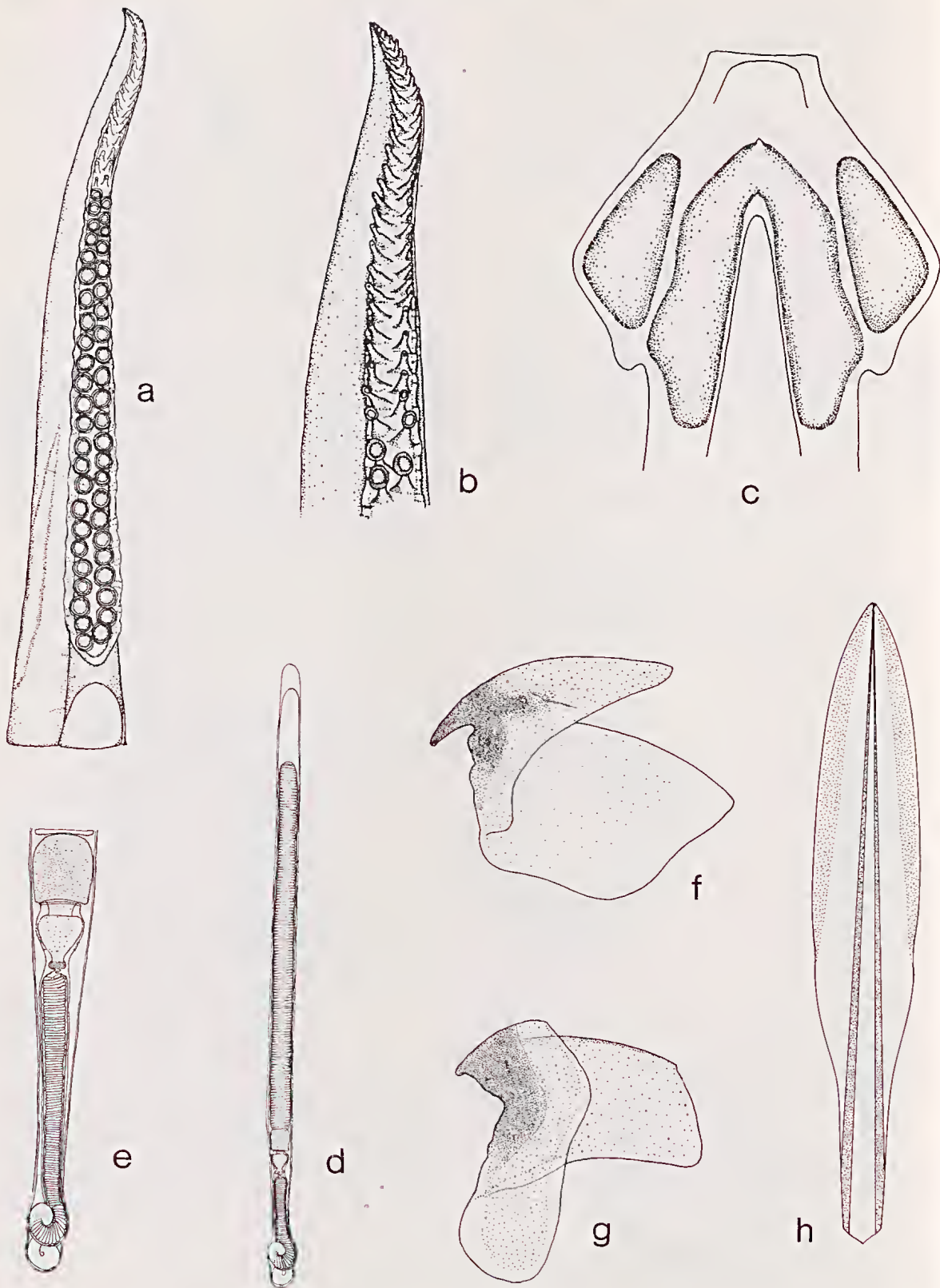


TABLE 1
MEANS, STANDARD DEVIATIONS AND RANGES OF INDICES OF *Sepioteuthis lessoniana* FROM AUSTRALIA

Index	n	MALES			n	FEMALES		
		Mean	S.D. (n-1)	Range		Mean	S.D. (n-1)	Range
ML(mm)				104-356				85-250
MWl	13	30.3	2.7	24-35	7	32.3	3.4	26-35
HLl	13	23.1	3.4	17-29	7	23.6	1.1	22-25
HWl	13	24.6	2.7	21-31	7	24.8	1.7	22-27
FLl	13	90.5	2.5	86-94	7	90.6	2.6	87-93
FWl	13	62.7	7.6	53-80	7	64.9	7.0	58-77
FL/FW	13	146.2	16.7	115-168	7	140.7	12.9	121-157
AL _I l	12	29.6	2.4	27-33	7	27.7	2.2	25-31
AL _{II} l	13	39.0	3.5	34-48	7	37.0	3.9	32-43
AL _{III} l	13	47.1	2.7	44-53	6	44.6	3.9	40-49
AL _{IV} l	12	41.8	3.4	36-48	7	41.4	2.9	37-46
HAl	11	42.3	2.9	37-51				
HCl	11	29.3	2.5	25-34				
TLl	13	102.7	15.7	82-135	7	97.9	14.8	76-115
CLl	13	39.3	4.3	33-44	7	38.6	5.4	35-49
AS _I l	13	0.83	0.08	0.6-0.9	7	0.86	0.11	0.8-0.9
AS _{II} l	13	1.01	0.09	0.8-1.1	7	1.02	0.08	0.9-1.1
AS _{III} l	13	1.22	0.10	1.0-1.3	7	1.19	0.12	1.0-1.3
AS _{IV} l	13	0.86	0.07	0.7-1.0	7	0.89	0.05	0.8-0.9
CSl	13	1.64	0.28	1.0-1.9	7	1.46	0.24	1.2-1.8
GWl	13	18.3	1.2	15-20	7	19.5	1.8	18-22
RLl	13	19.3	1.7	16-22	7	16.5	2.2	13-20
RWl	13	6.54	0.43	5.2-7.1	7	6.60	0.51	5.9-7.4
SL(mm)	11			6.8-14.5				
SLl	11	4.84	0.60	4.0-5.8				
SRl	11	75.4	1.9	72-79				
SWl	11	4.61	0.40	3.8-5.1				

continuous posteriorly, extend for 86-94% of ML, less in very small specimens, widest in their posterior third (Fig. 1a, b); anterior lobes small, posterior margins well rounded, anterolateral margins only slightly convex. Funnel large, very stout; dorsal funnel organ (Fig. 2c) with broad limbs, expanded in anterior and posterior thirds, taper to blunt tips posteriorly; anterior end very blunt, small apical papilla present; ventral pads of funnel organ about two-thirds length of dorsal organ, broader posteriorly. Funnel valve subterminal, rounded with steep shoulders.

Head and eyes large, olfactory crest prominent, preocular pore present adjacent to base of third arm. Arms moderately long, order III, IV, II, I, robust, tapering evenly to fine tips. Arm I triangular in section with an aboral keel; Arm II with an aboral keel along its entire length; Arm III broad, with a thick, low aboral swimming keel; Arm IV lacks an aboral keel, broad tentacular sheath present dorsally, this may be distorted and narrowed proximally by ridges in the sheath musculature (Fig. 2a). Trabeculate protective membranes on Arms I-III very well developed, trabeculae arise between sucker bases, become diffuse at edge of

membranes. Both membranes on Arm I equal in height, dorsal membranes on Arms II and III lower than ventral membranes. Membranes on Arm IV low, ventral membrane lower, edges scalloped; trabeculae weaker than on Arms I-III. Arm suckers increase in size from proximal end distally, largest at one quarter of arm length from proximal end, diminish evenly in size distally becoming minute at tip; arm suckers lack fleshy protuberances seen on club manal suckers. Largest arm sucker rings on all arms with 17-28 teeth on complete circumference; distal teeth long, acutely pointed; proximal teeth small, blunt. Teeth on distal sucker rings fewer, often truncate (Fig. 1f).

Left ventral arm of males *hectocotyliised* (Fig. 2a, b) by modification of distal 25-34%; 22-26 pairs of suckers modified into long, fleshy papillae slightly larger in dorsal row; each papilla has a minute sucker at its apex, suckers on distal papillae lack sucker rings. On proximal portion of arm, 23-31 pairs of suckers remain unmodified; each sucker ring bears 20-28 teeth similar to those on other arms. Trabeculate protective membranes on unmodified portion of arm similar to those on right ventral arm; along modified portion ventral membrane

Fig. 2—*Sepioteuthis lessoniana* Lesson. a-e, male, NMVF31555, 155 mm ML. a, left ventral arm. b, hectocotyliised portion of left ventral arm. c, funnel organ. d, spermatophore. e, oral end of spermatophore. f-g, male, NMVF31557, 356 mm ML. f, upper beak. g, lower beak. h, gladius; male, NMVF31576, 217 mm ML.

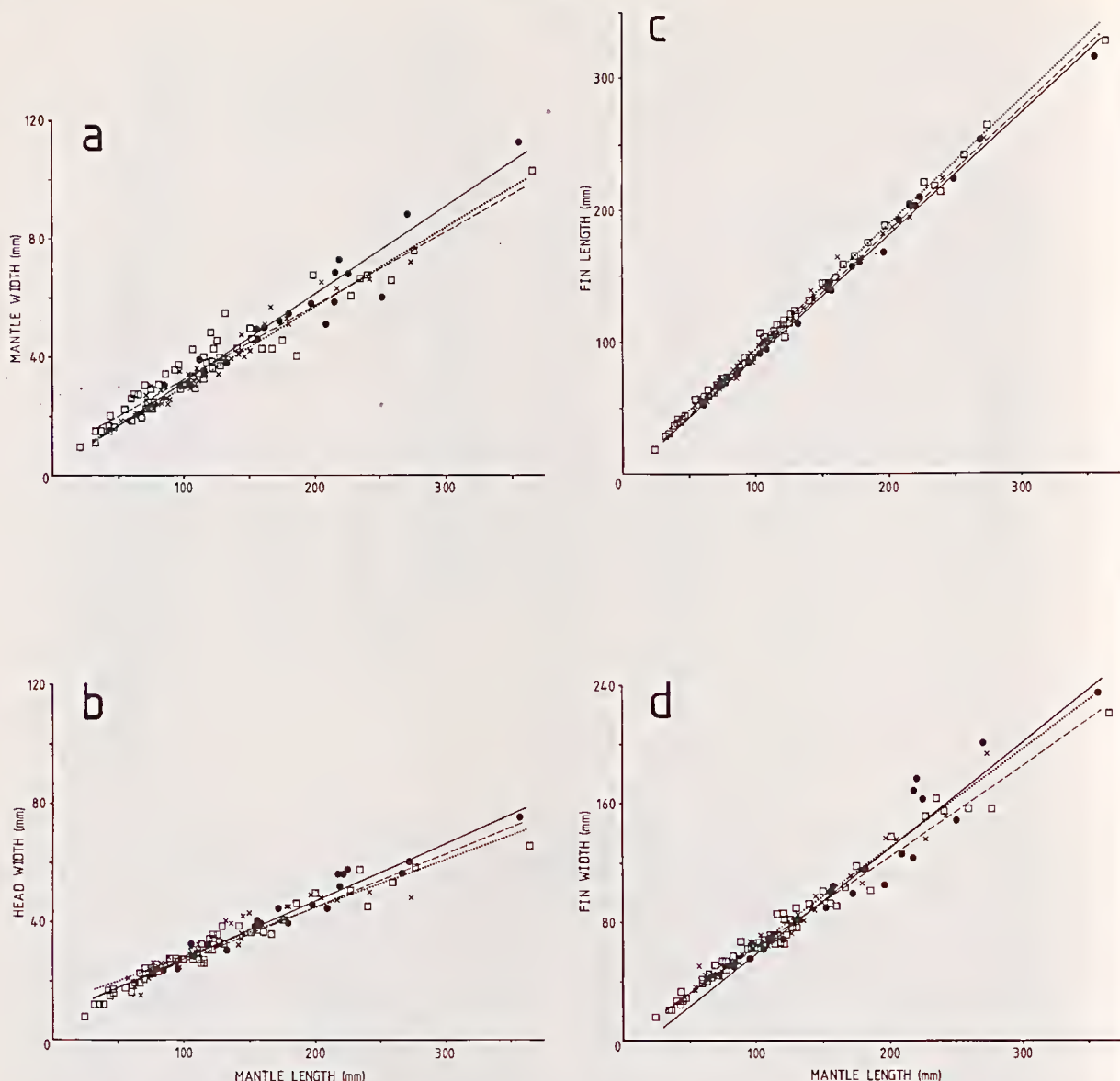


Fig. 3—Comparison of morphological parameters of *Sepioteuthis lessoniana* from Australia, Indonesia and the Philippines.

Australian sample—solid lines, solid dots.

Indonesian sample—dashed lines, hollow squares (measurements from Adam 1939).

Philippines sample—dotted lines, crosses (measurements from Voss 1963 and NMVF31764).

Regression data and comparisons of lines are given in Table 2.

continues to arm tip, dorsal membrane continues for only one-third to one-half hectocotylus length. *Tentacles* moderately long, robust; stalks naked. Clubs large, expanded (Fig. 1c); carpus and manus not distinct from each other, dactylus slender. Suckers on carpus biserial for proximal 1-2 pairs then tetraserial; manal suckers moderately large, possess finger-like fringes on outer margins, better developed on marginal suckers (Fig. 1d, e); median suckers 1.1-1.5 times diameter of marginal suckers; dactylus suckers small, decrease in

size from ventral to dorsal rows; distal tip slightly expanded, small naked patch present between median sucker rows at tip. Aboral swimming keel arises along the carpus, expands distally and terminates abruptly at tip; keel thickened along attachment to club. Trabeculate protective membranes arise from the proximal portion of the carpus, well developed; dorsal membrane terminates at the proximal portion of the dactylus; ventral membrane continues along dactylus, terminates at club tip; trabeculae on both membranes

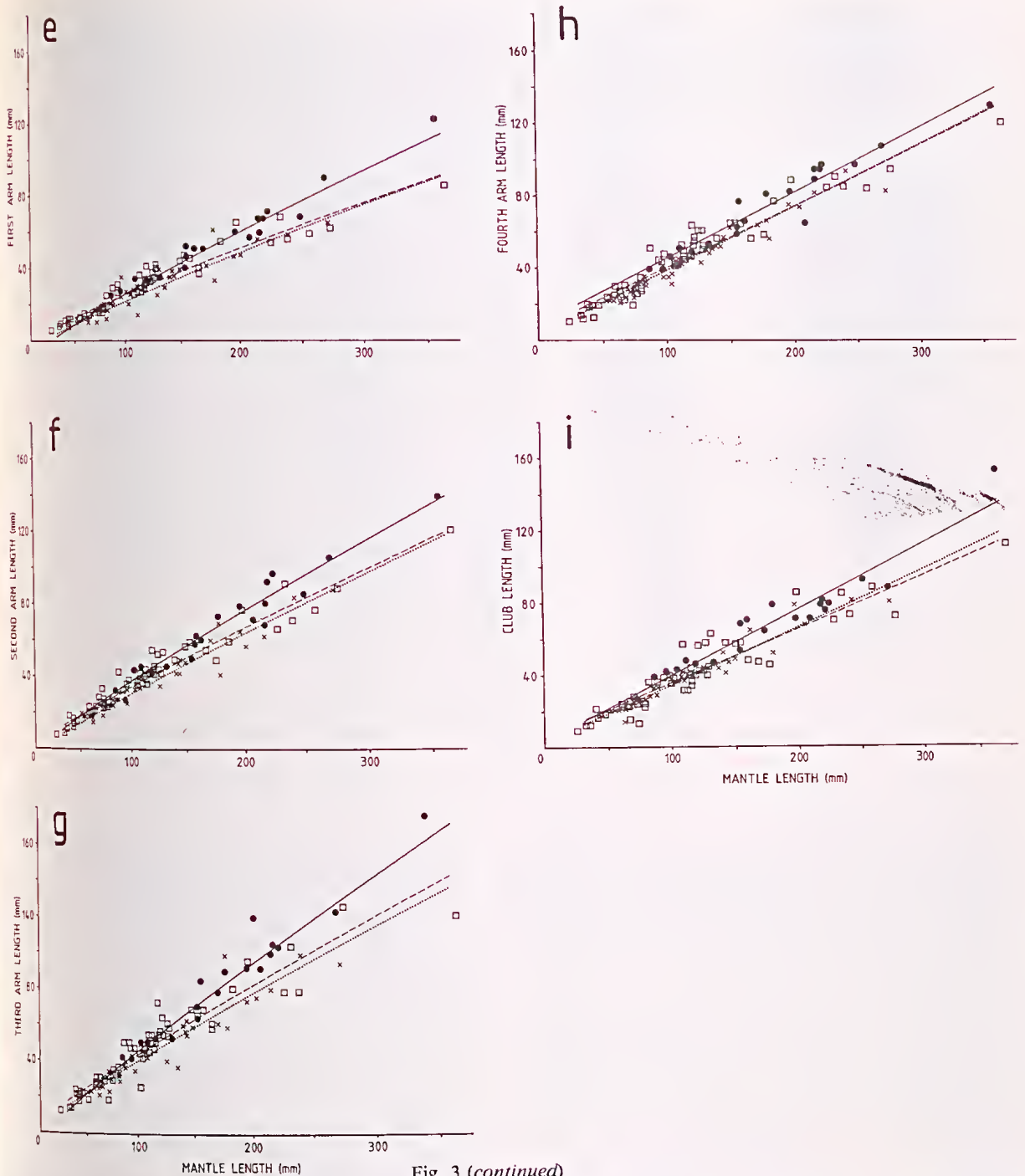


Fig. 3 (continued)

arise between sucker stalks, broad, strong, slightly diffuse at edges of membranes.

Sucker rings of the carpus with 13-23 acutely pointed teeth, longer and more acute on distal margins; manal sucker rings with 13-24 strong, sharp, well spaced teeth, larger and more acute on distal margins of median suckers and on outer margins of marginal suckers. Sucker rings of dactylus with 15-23 sharp teeth, teeth

larger on ventral suckers, fewer on distal suckers; suckers of terminal expansion of dactylus with low, rounded teeth or lacking dentition. *Buccal membrane* with seven lappets, supported by strong connectives, ventral lappets generally lower than others; each lappet bears 0-10 small suckers, fewer on ventral lappets; each sucker ring with 15-25 minute, truncate teeth, larger on distal margins. Buccal seminal receptacle present on oral

TABLE 2
COMPARISON OF MORPHOLOGICAL PARAMETERS OF *Sepioteuthis lessoniana* FROM AUSTRALIA, INDONESIA
AND THE PHILIPPINES

Regression data relating to Fig. 3. $y = bx + a$; n = no. of individuals per sample; b = regression coefficient; a = vertical intercept; R^2 = coefficient of determination; sig. diff. = significant difference between the lines indicated by the parentheses, with respect to slope or elevation. Regression coefficients in all cases are significant at the 0.1% level.

Ref. Fig. 3	Function	Sample	n	b	a	R^2	sig. diff.
a	MW-ML	Indon.	56	0.2491	7.2989	0.9243	
		Aust.	20	0.2949	2.1962	0.9222	$p < 0.05$ (slope)
		Philipp.	41	0.2634	4.2409	0.9669	$p < 0.05$ (elev.)
b	HW-ML	Indon.	56	0.1785	8.7720	0.9419	
		Aust.	20	0.1957	8.0775	0.9458	$p < 0.02$ (elev.)
		Philipp.	34	0.1662	11.4587	0.8699	N.S.
c	FL-ML	Indon.	56	0.9275	-0.2117	0.9966	
		Aust.	20	0.9234	-2.5962	0.9950	$p < 0.01$ (elev.)
		Philipp.	41	0.9200	0.6374	0.9972	$p < 0.02$ (elev.)
d	FW-ML	Indon.	56	0.6089	1.9452	0.9773	
		Aust.	20	0.7194	-13.4932	0.9206	$p < 0.005$ (slope)
		Philipp.	41	0.6512	-0.5959	0.9779	N.S.
e	AL _I -ML	Indon.	56	0.2464	1.2267	0.9322	
		Aust.	19	0.3430	-9.1813	0.9598	$p < 0.001$ (slope)
		Philipp.	41	0.2586	-2.8803	0.8940	$p < 0.001$ (slope)
f	AL _{II} -ML	Indon.	55	0.3227	2.8631	0.9428	
		Aust.	20	0.3933	-2.2372	0.9565	$p < 0.002$ (slope)
		Philipp.	41	0.3317	-1.4673	0.8772	$p < 0.05$ (slope)
g	AL _{III} -ML	Indon.	56	0.3814	5.4510	0.9347	
		Aust.	19	0.4894	-4.2879	0.9744	$p < 0.001$ (slope)
		Philipp.	41	0.3684	3.5439	0.9010	$p < 0.001$ (slope)
h	AL _{IV} -ML	Indon.	56	0.3383	6.6125	0.9185	
		Aust.	19	0.3640	8.4895	0.9604	$p < 0.002$ (elev.)
		Philipp.	41	0.3506	3.5541	0.9253	$p < 0.001$ (elev.)
i	CL-ML	Indon.	53	0.2972	5.9639	0.9036	
		Aust.	20	0.3643	3.3195	0.9107	$p < 0.02$ (slope)
		Philipp.	38	0.3198	2.7019	0.9370	$p < 0.001$ (elev.)

surface between ventral lappets of females, very well developed; large white, glandular organ lies just under surface of membrane, opens through a narrow, elongate aperture; small papilla present at aboral end of aperture. Rostrum of *upper beak* (Fig. 2f) sharply pointed, long, curved; width slightly less than or equal to length; rostral margin and tip dark brown to black, dark pigmentation expanded posteriorly from jaw angle, remaining area of rostrum and hood lightly pigmented. Hood length about 3.5-6.0 times rostral length; wing length about 1.5-2.3 times rostral length, cutting edge of wing irregular, a large tooth present near jaw angle. Crest curved, lateral wall large, lightly pigmented anteriorly (at least on specimens larger than 104 mm ML) posterior margin with a shallow indentation, posterior margin of lateral wall unpigmented. Rostrum of *lower beak* (Fig. 2g) long, pointed, black cutting edge of rostrum straight, irregularly serrated, rostral width slightly greater than or equal to rostral length; wing length about 2.3-3.7 times rostral length; cutting edge of wing straight, irregularly serrated; margin of wing unpigmented, remaining area of wing lightly pigmented. Hood heavily pigmented anteriorly, black, lightly pigmented posteriorly. Crest curved, crest length about

3.5-4.0 times rostral length; lateral wall length about 4-5 times rostral length, lightly pigmented with transparent margins. *Radula* (Fig. 1g) with seven transverse rows of teeth; rhachidian tooth stout with straight edges, lateral cusps high, blunt; first lateral stout, similar length to rhachidian, lateral cusps high, blunt; second lateral slightly curved, stout, 1.5-2.0 times length of rhachidian, no cusps; third lateral curved, stout, 2.0-2.5 times length of rhachidian, tip blunt; marginal plates elongate, narrower in their outer third. *Gladius* (Fig. 2h) broad, vane widest in its posterior third, conspicuously dilated posteriorly to attachment of funnel adductor muscles; vane thickened in a broad band immediately median to edges, extending from attachment of funnel adductor muscles to posterior tip, vane edge not thickened. Free rachis short, longer in small specimens, broad, strong; median groove rounded, supported by strongly thickened lateral rods for length of gladius. *Spermatophores* of Australian specimens (Figs 2d, e, 4a, b) small, sperm mass comprises 72-79% of total length. Cement body clearly bipartite; aboral end rounded, stout, connected to oral end by a narrow neck; oral end flask shaped with distinct shoulders tapering evenly to a small, dark terminal dilation. Middle tunic spirally

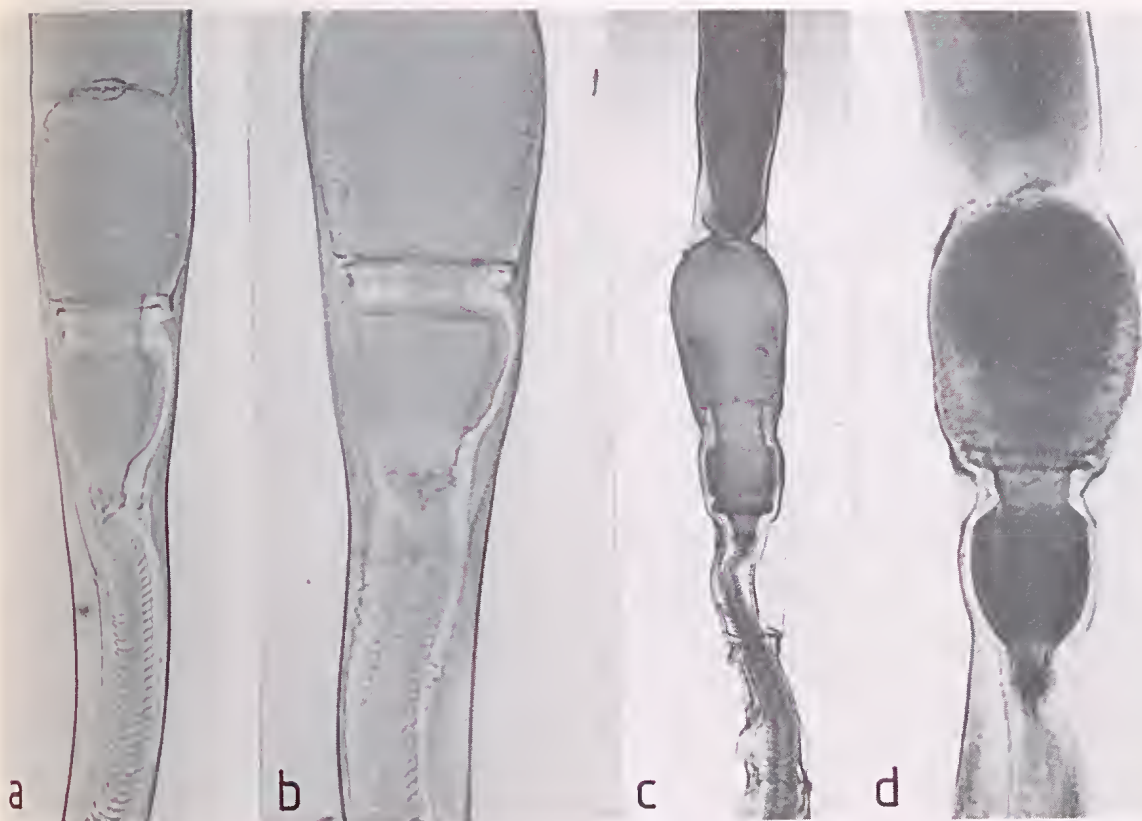


Fig. 4—*Sepioteuthis lessoniana* Lesson. Geographic variation in spermatophore cement bodies from Australia, Philippines and Vietnam. a, NMVF31552, 118 mm ML, N.E. Australia. b, NMVF31555, 155 mm ML, N.W. Australia. c, NMVF31764, 273 mm ML, Philippines. d, ZMC, 112 mm ML, Vietnam.

sculptured along oral end of cement body, forms a distinct shoulder opposite cement body neck; ejaculatory apparatus tightly coiled, forms several large coils in the oral swelling of spermatophore. Specimens in isopropyl alcohol cream coloured; dorsal surface of body and fins closely covered in large purplish chromatophores, in some specimens a darker median line or irregularly placed, short transverse dashes are present; chromatophores on ventral body surface less concentrated, absent on ventral fin surfaces. Head and aboral aspects of arms and tentacles also closely covered with chromatophores, less concentrated ventrally; dark patch present dorsal to each eye. No photophores present on this species. The smallest male examined which had well developed spermatophores present in the needhams sac was 120 mm ML, hectocotylation is evident in immature males as small as 71 mm ML. The nidamental glands of females begin rapid enlargement from 160-200 mm ML.

HOLOTYPE: Not traced. Muséum National d'Histoire Naturelle, Paris?

TYPE LOCALITY: 'Le havre de Doréry'=(?) Dore Bay, West Irian, approximately 0°51'S., 134°01'E.

DISTRIBUTION: A neritic species widely distributed in the Indian and Pacific Oceans, from Japan (Okutani 1973)

to Australia, and the Red Sea (Adam 1973) to the Hawaiian Islands (as *S. arctipinnis*) (Berry 1912); not recorded from the eastern Pacific coast of America. Records from New Zealand by Gray (1849, p. 80) not confirmed. In Australia this species is recorded from northern coastal waters to depths of 110 m (Fig. 8a). Southern most records are: eastern coast 27°12'S. (NMVF31611); western coast 28°48'S. (WAM1420-83).

GEOGRAPHIC VARIATION: The Australian sample could be separated morphometrically from the Indonesian and Philippine samples by comparison of any of the parameters: mantle width, fin length, fin width, lengths of Arms I-IV and tentacle club length. Head length and gladius width were the only parameters tested which did not show a separation. The best separation of Australian and Asian samples was found by comparison of arm lengths (Fig. 3e-h). In general, mature specimens from Australia are slightly broader, a difference reflected in mantle, head and fin width, and the arms and tentacle clubs are slightly longer.

Differences in the shape of cement body of the spermatophore were also apparent. Specimens from the east and west coasts of Australia are identical, the cement body has a flask shaped oral end, evenly tapered (Fig. 4a, b). Specimens from the Philippines (Fig. 4c) have a

larger aboral part to the cement body; the oral part is stout with a slight constriction at half its length, a well developed shoulder is present orally, adjacent to the terminal dilation. The single specimen examined from Vietnam (Fig. 4d) is similar to Australian examples but has a larger aboral part to the cement body and less marked aboral shoulders on the oral part.

REMARKS: *Sepioteuthis lessoniana* from Australia matches closely with the detailed descriptions of Sasaki (1929, p. 127), Adam (1939, p. 2) and Voss (1963, p. 77). The transverse dashes seen on the dorsal surface of some specimens were described by Ikeda (1933) and Adam (1938) as a secondary sexual characteristic of males. These markings were only observed on Australian male specimens but the corresponding markings described by the above authors on females were not observed. The morphometric variation shown by this species was noted by Adam (1939), who examined a total of 84 specimens and gave detailed measurements for 59, from various Indonesian localities, some from as close to Australia as Timor. This is the first time however, that material has been statistically compared from widely separated geographic locations where some isolation may be expected. The results indicate that the Australian material may belong to a population morphologically separable from its nearest northern neighbours and this is supported by differences in spermatophore morphology. This may be due to distance factors alone, but areas of deeper water separating sample localities would also have isolating effects over shorter distances on a neritic species. Further analysis of variation on a finer scale, such as within the large ranges of the species within Australian and Indonesian waters would require a much larger sample than that available to the present study.

Sepioteuthis australis Quoy & Gaimard 1832

Figs 5-7, 8b, 9-10

1832 *Sepioteuthis australis* Quoy & Gaimard, p. 77, pl. 4, fig. 1.

1873 *Sepioteuthis major* Hutton, p. 3 (non Gray, 1828).

1880 *Sepioteuthis bilineata* Hutton, p. 3.

1909 *Sepioteuthis mauritiana*; Meyer, p. 329, figs 1-2 (non Quoy & Gaimard, 1832).

DIAGNOSIS: Fins widest at about half their length; buccal membrane well developed, suckers present on all lap-pets. Restricted to southern Australia and New Zealand waters.

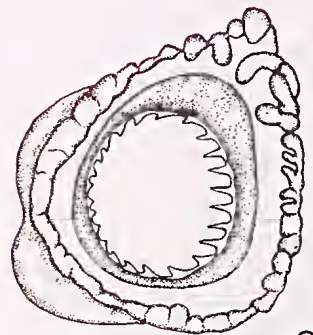
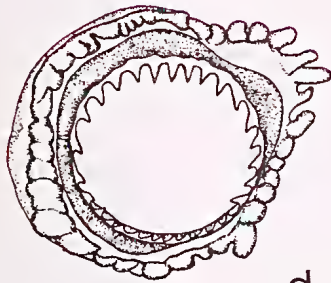
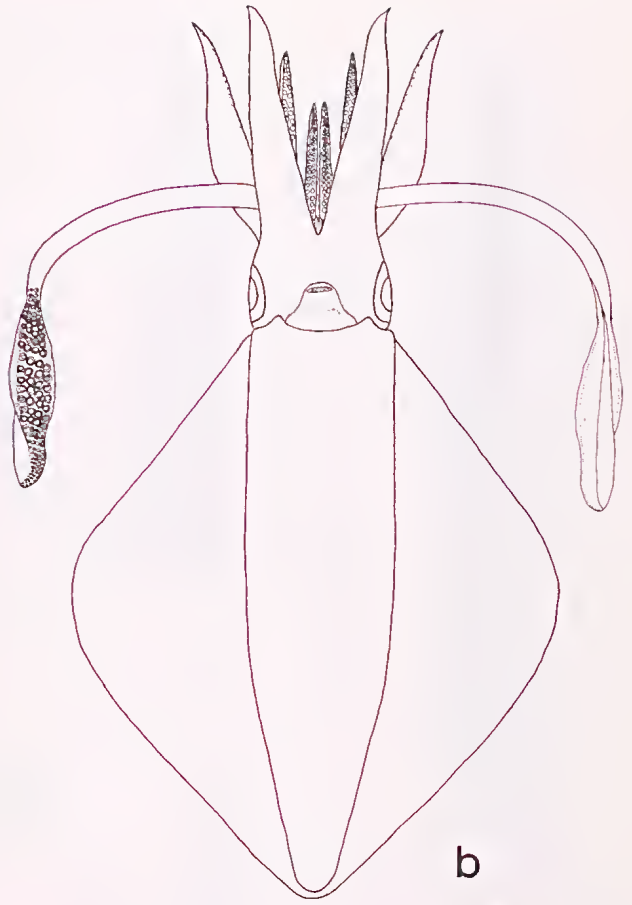
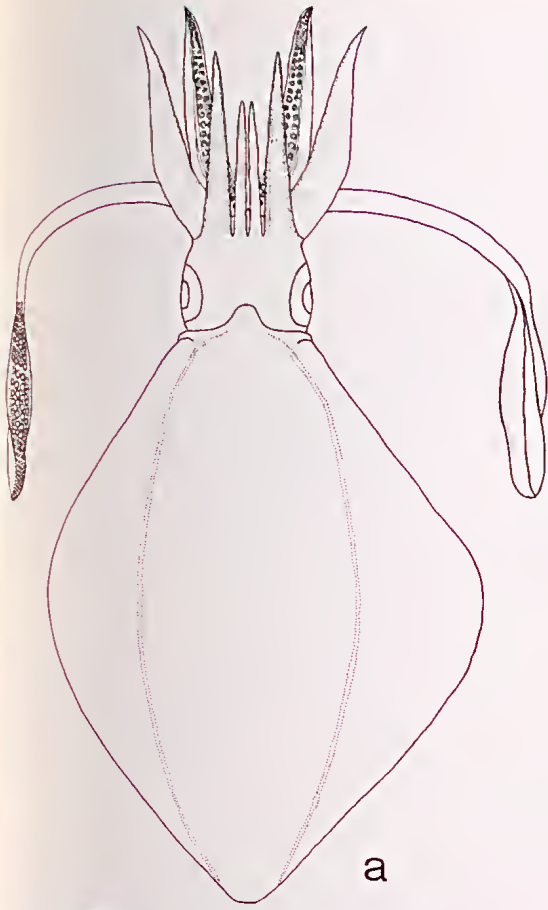
MATERIALS EXAMINED: See APPENDIX 6.

DESCRIPTION: *Mantle* stout, broader in New Zealand specimens, tapers to a blunt tip posteriorly; anterior dorsal lobe prominent, rounded; ventrolateral lobes low, pointed. *Fins* large, rhombic (Fig. 5a, b) broadest at midpoint, continuous posteriorly; extend for 78-96%

of mantle length, less in very small specimens; anterolateral and posterolateral margins straight or slightly convex, anterior lobes small. *Funnel* large, broad, strongly tapered, dorsal funnel organ (Fig. 6c) with broad limbs, tapering posteriorly to a blunt tip, becoming narrow anteriorly with a raised fleshy pad at tip and a well developed apical papilla. Ventral pads about half length of dorsal organ, dorsal margin nearly straight, pads widest just posterior to midpoint; funnel valve subterminal, rounded. *Head* and eyes large, olfactory crest prominent, preocular pore present adjacent to base of third arm. *Arms* moderately long, all robust, order III, IV, II, I or IV, III, II, I, taper evenly to fine tips. Arm I triangular in section with a well developed aboral keel disappearing proximally; Arm II with an aboral keel along its entire length. Arm III broad, triangular in section well developed aboral keel present along entire length. Arm IV lacks an aboral keel, dorsally a broad tentacular sheath is present, somewhat distorted proximally in large specimens by muscular ridges in the sheath (Fig. 6a), ventrally a low flange is present on distal two-thirds of arm. Trabeculate protective membranes on Arms I-III well developed, dorsal and ventral membranes equal in height; trabeculae arise between sucker bases, strong at base, become diffuse at edges of membranes. Membranes on Arm IV less well developed, slightly scalloped at edges, ventral membrane lower than dorsal membrane; trabeculae weaker than on Arms I-III. *Suckers* largest at about one-quarter of arm length from proximal end, diminish evenly in size distally, becoming minute at distal tip; largest suckers on all arms slightly smaller in New Zealand specimens; arm suckers lack fleshy protuberances seen on club manal suckers. Largest arm sucker rings on Arms I-IV with 18-32 well spaced teeth on complete circumference; distal teeth moderately short, sharp or peg like; proximal teeth small, conical or blunt. Teeth on distal sucker rings of all arms fewer, truncate or rounded. Left ventral arm of males *hectocotylised* by modification of distal 18-22% (Fig. 6a, b); 24-28 pairs of suckers in this region modified into long, fleshy papillae slightly larger in the dorsal row, each with a minute sucker at its apex. Terminal portion of hectocotylus on large, mature males attenuate, weak; distal 9-10 pairs of papillae greatly reduced, suckers at tips similar size to most distal suckers on right ventral arm; tentacular sheath becomes very weak and ventral flange disappears along attenuate tip. Proximal portion of the arm with 32-41 pairs of unmodified suckers, sucker ring dentition similar to that of other arms. Trabeculate protective membranes along unmodified portion of arm similar to those on right ventral arm; along modified portion membranes are reduced, strongly scalloped, fused to papillae; continuing to distal tip on both sides.

Tentacles moderately long, robust, stalks naked. *Clubs* (Fig. 5c) large, expanded, slightly smaller in New

Fig. 5—*Sepioteuthis australis* Quoy & Gaimard; male, NMVF30876, 214 mm ML. a, dorsal view. b, ventral view. c, right tentacular club. d, largest median manal sucker of club. e, largest marginal sucker of club. f, largest sucker ring from third right arm. g, radula. (d-f orientated distal aspect to top of page).



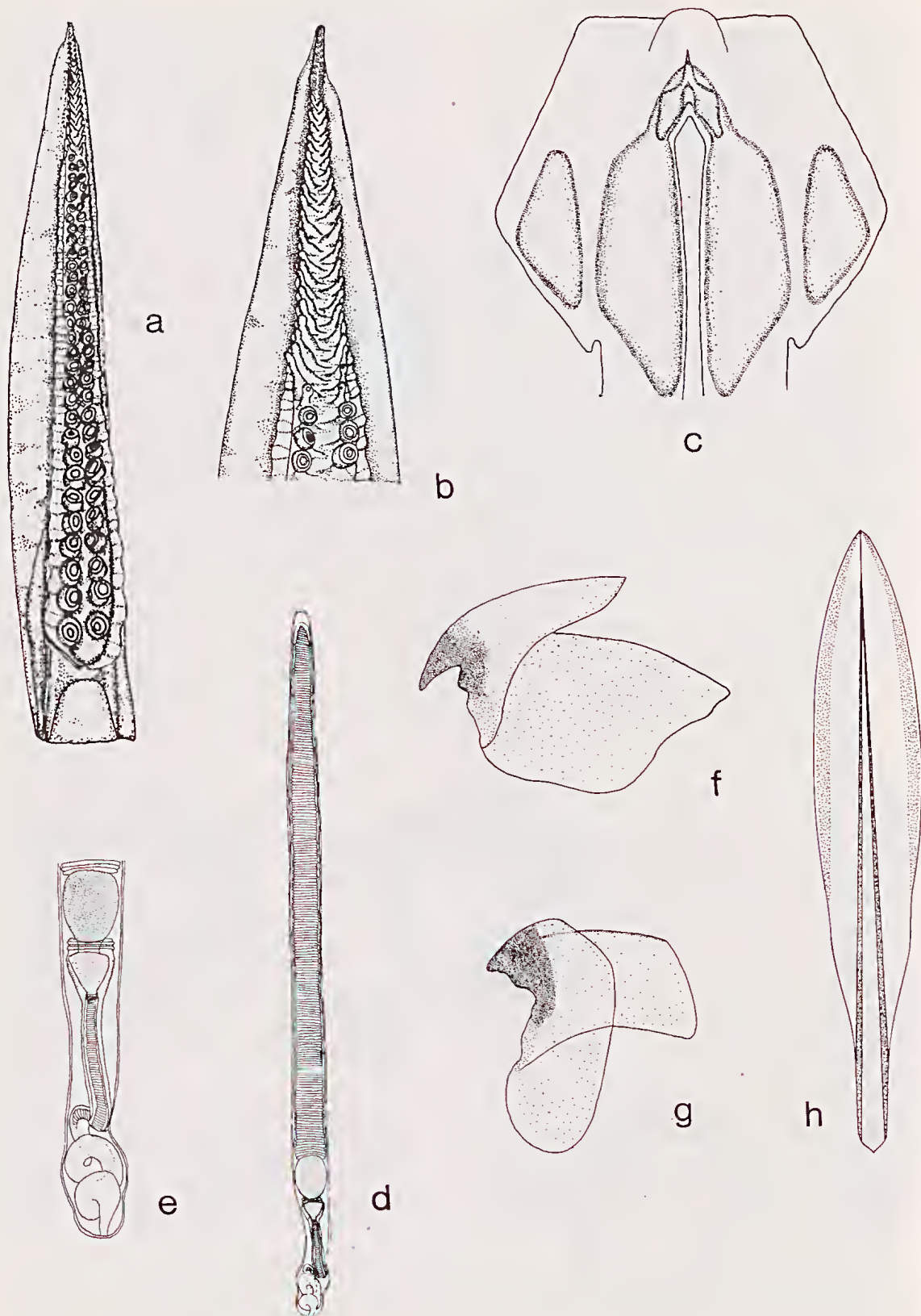


TABLE 3
MEANS, STANDARD DEVIATIONS AND RANGES OF INDICES OF *Sepioteuthis australis* QUOY & GAIMARD FROM AUSTRALIA AND NEW ZEALAND

Index	n	Mean	S.D. (n - 1)	Range	n	Mean	S.D. (n - 1)	Range
ML(mm)	17			33-355	15			43-256
MW1	17	29.4	4.7	23-39	15	29.8	4.6	23-40
HL1	17	21.9	4.4	17-30	15	22.3	2.1	20-27
HW1	17	26.7	4.9	18-34	15	26.8	3.5	22-33
FL1	17	88.1	4.3	78-93	15	89.3	3.1	84-96
FW1	17	74.3	6.7	65-89	15	75.5	7.2	62-87
FL/FW	17	119.4	9.8	102-135	15	119.5	12.8	102-146
AL _I 1	17	24.0	3.9	16-30	15	24.1	2.2	21-29
AL _{II} 1	17	34.2	3.9	26-29	15	34.5	2.7	31-41
AL _{III} 1	17	41.6	5.8	33-52	15	41.3	3.7	33-48
AL _{IV} 1	17	39.5	5.9	30-49	15	40.8	3.5	36-48
HA1	4	37.5	3.1	35-41				
HC1	4	20.3	1.5	18-22				
TL1	17	95.2	23.7	65-132	15	90.1	24.1	64-128
CL1	17	32.2	4.1	26-42	15	32.4	3.4	27-38
AS _I 1	17	0.51	0.10	0.3-0.7	15	0.54	0.07	0.4-0.7
AS _{II} 1	17	0.72	0.13	0.5-0.9	15	0.75	0.10	0.6-0.9
AS _{III} 1	17	0.85	0.15	0.6-1.2	15	0.89	0.10	0.7-1.1
AS _{IV} 1	17	0.61	0.12	0.4-0.8	15	0.65	0.06	0.6-0.8
CS1	17	1.15	0.32	0.6-1.7	15	1.27	0.26	0.9-1.8
GW1	17	18.6	1.8	16-21	15	18.3	2.0	15-22
RL1	17	19.3	1.9	16-24	14	18.6	1.8	16-22
RW1	17	5.54	0.43	5.0-6.3	14	5.66	0.46	4.9-6.6
SL(mm)	7			15-23				
SL1	7	6.36	0.59	5.2-7.0				
SR1	7	77.6	2.5	73-80				
SW1	7	5.29	0.28	4.8-5.6				

Zealand specimens, carpus and manus not distinct from each other, dactylus slender, slightly expanded at tip. Suckers on carpus biserial for proximal 1-2 rows, tetraseriate distally; manal suckers moderately large, slightly smaller on New Zealand specimens, possess finger-like fleshy fringes on outer margins, better developed on marginal suckers (Fig. 5d, e); median manal suckers 1.1-1.5 times diameter of marginals; dactylus suckers small becoming minute at tip, decrease in size from ventral to dorsal rows; distal tip slightly expanded, small naked patch present between median sucker rows at tip. Aboral swimming keel arises along the carpus, expands distally and terminates abruptly at tip, keel slightly thickened along attachment to club. Trabeculate protective membranes well developed, arise along proximal portion of carpus, trabeculae broad, strong, arise between sucker bases, diffuse at edges of membranes; dorsal membrane terminates along proximal portion of dactylus, ventral membrane continues along dactylus to distal tip.

Sucker rings of carpus with 18-30 pointed or truncate teeth on complete circumference, larger and more pointed distally. Sucker rings of manus also with 18-30 sharp teeth, larger distally on median suckers and

marginally on marginal suckers; largest teeth of marginal suckers generally larger than those of median suckers. Sucker rings of dactylus with 22-26 sharp teeth, fewer on distal suckers, teeth larger on ventral suckers, larger on ventral aspects of all suckers; sucker rings of terminal expansion of dactylus lacking dentition. *Buccal membrane* with seven lappets supported by strong connectives, lateral lappets strongest, ventral lappets generally lowest; each lappet bears 0-9 small suckers each bearing 20-25 minute, truncate teeth, larger on distal margins. Buccal seminal receptacle present on oral surface between ventral lappets of females, very well developed; large, transversely grooved spermathecal pad is only partially enclosed by folds of buccal membrane, aboral tip of pad free but lies closely against membrane.

Upper beak (Fig. 6f) with rostrum sharply pointed, long, curved, width approximately equal to length; rostral margin and tip dark brown to black, dark pigmentation expanded posteriorly to rostral margin and jaw angle, remaining area of rostrum and hood lightly pigmented. Hood length about 4-6 times rostral length; wing length about 1.5-2.4 times rostral length, cutting edge of wing straight, irregularly serrated, a large tooth present near jaw angle. Crest curved, lateral

Fig. 6—*Sepioteuthis australis* Quoy & Gaimard; male, NMVF30876, 214 mm ML. a, left ventral arm. b, hectocotylied portion of left ventral arm. c, funnel organ. d, spermatophore. e, oral end of spermatophore. f, upper beak. g, lower beak. h, gladius.

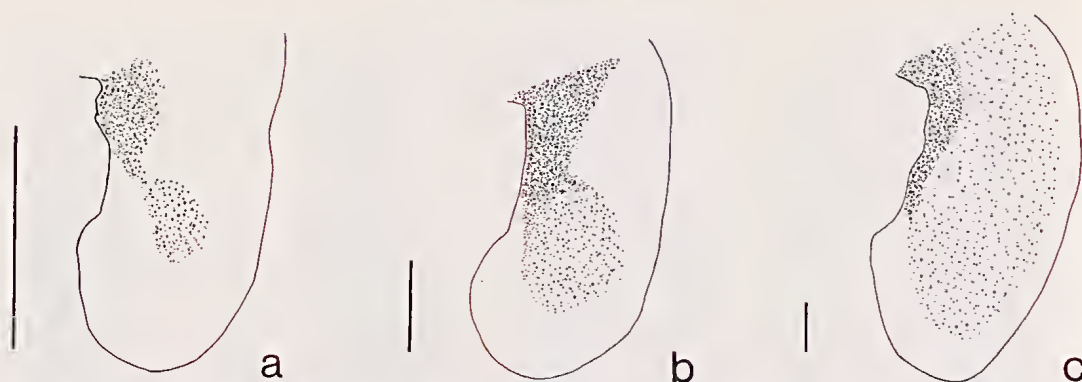


Fig. 7—*Sepioteuthis australis* Quoy & Gaimard. Development of darkening on beak wings. a, female, NMVF31567, 43 mm ML. b, male, NMNZM9829, 107 mm ML. c, male, NMVF30876, 214 mm ML. Scale bars equivalent to 2 mm.

wall large, lightly pigmented anteriorly on all specimens examined, posterior margin with a shallow indentation, lateral wall margin unpigmented. **Lower beak** (Fig. 6g) rostrum long, pointed, black, width approximately equal to length; cutting edge of rostrum straight, irregularly serrated. Wing 1.5–2.4 times rostral length, pigmentation occurs on animals of at least 43 mm ML: wing pigmentation (Fig. 7) begins as a lightly pigmented spot, expands gradually through a club shaped pigmented area, to the final stage of uniformly pigmented wing with transparent margins at about 200 mm ML. Hood heavily pigmented anteriorly, lightly pigmented posteriorly; crest curved, crest length about 3.0–4.5 times rostral length; lateral wall length about 3.5–6.0 times rostral length, lightly pigmented with transparent margins.

Radula (Fig. 5g) with seven transverse rows of teeth; rhachidian tooth stout with straight edges, lateral cusps high, sharp, slightly curved; first lateral about 90% of height of rhachidian, lateral cusp sharp, slightly curved; second lateral nearly straight, about 1.6 times height of rhachidian, stout, tip blunt, no cusps; third lateral curved, about 2.2–2.4 times height of rhachidian, tip blunt, no cusps; marginal plates ovoid. **Gladius** (Fig. 6h) broad, wider in New Zealand specimens; vane dilated posterior to attachment of funnel adductor muscles, widest at about half its length; thickened band immediately medial to vane edge extends from point of attachment of funnel muscles to posterior tip, vane edge unthickened. Free rachis short, moderately broad, strong, rounded central groove supported by thickened lateral rods which become weaker and disappear posteriorly.

Spermatophores (Figs 6d, e, 10) from the vicinity of the type locality with bipartite cement body; aboral end elongate, stout, slightly narrower orally; oral end of cement body connected to aboral end by a stout neck, flask shaped, tapering evenly or with a slight median bulge to oral extremity; oral extremity of cement body slightly dilated. Middle tunic commences along aboral part of cement body neck; may form two annular ridges along neck, strongly spirally sculptured along oral end

of cement body, less distinctly sculptured along ejaculatory apparatus. Ejaculatory apparatus strongly coiled, several coils in oral dilation of spermatophore. Badly damaged spermatophores from a single specimen from the northwestern extremity of this species range (WAM 785–81) still had intact cement bodies; these resembled specimens from southeastern Australia but had a slightly more elongate aboral end of the cement body. Spermatophores from New Zealand specimens (NMVF31752) similar in relative size to those from Australia, but with slight differences in the form of the cement body (Fig. 10b). Aboral end of cement body short, almost round, connected to oral end by a stout neck; oral end ovoid, lacking distinct shoulders adjacent to neck, oral extremity expanded. Middle tunic with a broad collar along cement body neck, lacks annular ridges, slightly constricted along oral end of neck; tunic spirally sculptured along oral end of cement body. Ejaculatory apparatus similar to Australian forms.

Specimens preserved in iso-propyl alcohol cream coloured; dorsal surface of mantle and fins closely covered in large, purplish chromatophores, more concentrated medially. Chromatophores on ventral surface of mantle less concentrated, ventral surfaces of fins lacking chromatophores. Specimens from northern limits of distribution generally darker coloured. Head and aboral aspects of arms and tentacles densely covered with small chromatophores, less concentrated ventrally; dark patches present over each eye. No photophores present in this species.

Males have well developed spermatophores in the needhams sac from about 200 mm ML. The smallest animal in which hectocotylation could be observed was 79 mm ML. The nidamental glands of females begin rapid enlargement at 150–200 mm ML. As the largest male recorded was 355 mm ML and the largest females with large, egg filled ovaries were only 183 and 250 mm ML it seems likely that females do not achieve such a large size as males.

HOLOTYPE: MNHP 2.5.430. Sex unknown. 275 mm ML. Dried, fragmented remains of beaks only extant.

TABLE 4

COMPARISON OF MORPHOLOGICAL PARAMETERS OF *Sepioteuthis australis* FROM AUSTRALIA AND NEW ZEALAND

Regression data relating to Fig. 9. For explanation of abbreviations see Table 2. Regression coefficients in all cases are significant at the 0.1% level.

Ref. Fig. 9	Function	Sample	n	b	a	R ²	sig. diff.
a	MW-ML	Aust.	18	0.2446	2.4440	0.9827	p < 0.02 (slope)
		N.Z.	13	0.3057	2.7691	0.9395	
b	GW-ML	Aust.	18	0.1543	2.0862	0.9851	p < 0.001 (slope)
		N.Z.	14	0.2113	-1.1967	0.9860	
c	FW-ML	Aust.	18	0.6876	0.7665	0.9851	p < 0.02 (elev.)
		N.Z.	14	0.7665	2.4311	0.9635	
d	CL-ML	Aust.	18	0.3676	-3.9187	0.9868	p < 0.005 (slope)
		N.Z.	14	0.2893	1.4562	0.9446	
e	AS _I -ML	Aust.	18	0.0065	-0.0946	0.9692	p < 0.02 (slope)
		N.Z.	14	0.0052	-0.0417	0.9771	
f	AS _{II} -ML	Aust.	18	0.0092	-0.1443	0.9771	p < 0.002 (slope)
		N.Z.	14	0.0068	-0.0302	0.9539	
g	AS _{III} -ML	Aust.	18	0.0107	-0.1553	0.9821	p < 0.001 (slope)
		N.Z.	14	0.0074	-0.0466	0.9448	
h	AS _{IV} -ML	Aust.	18	0.0075	-0.0804	0.9573	p < 0.05 (slope)
		N.Z.	14	0.0059	-0.0109	0.9622	
i	CS-ML	Aust.	18	0.0163	-0.2635	0.9625	p < 0.001 (slope)
		N.Z.	14	0.0101	-0.0438	0.9195	

TYPE LOCALITY: Probably Western Port, Victoria.

DISTRIBUTION: *Sepioteuthis australis* is a neritic species around southern Australia, and northern New Zealand (Fig. 8b). The northernmost record on the west coast of Australia is from approximately 20°S, NW of Dampier (WAM 785-81); on the east coast it is from 27°40'S off Brisbane (NMVF31331). Bathymetric records range from 0-85 m. This species is common in sheltered southern waters such as Port Phillip Bay, Western Port, Gulf St. Vincent, and Spencer Gulf. In New Zealand the southernmost record is from 41°16'S, Nelson, Tasman Bay (Dell 1952).

GEOGRAPHIC VARIATION: Morphometric differences could be detected between southeastern Australian and New Zealand samples, by comparison of regressions of certain morphometric parameters plotted against mantle length (Fig. 9, Table 4). From Fig. 9a-c and Table 4, it is evident that New Zealand specimens are generally broader than those from SE Australia; this is reflected in the widths of the mantle, fins and gladius. The tentacular clubs of New Zealand specimens are also slightly smaller; this is reflected in the statistical differences in club length and club sucker diameter (Fig. 9d, i). Number of teeth on club suckers do not show any corresponding differences. Arm suckers on all arms are also smaller in New Zealand specimens (Fig. 9e-h), this is not reflected by any differences in number or form of the teeth on arm sucker rings. Other morphometric parameters compared which did not show any significant differences were head length, head width, fin length, and length of all arms.

Spermatophores from New Zealand also show differences to those from Australia (Fig. 10). New

Zealand specimens examined match closely in details of the cement body with the illustrations of Kirk (1884, pl. 6), which show the oral cement body without distinct shoulders at its junction with the cement body neck. These shoulders, giving the oral cement body a flask-like appearance are present in material examined from Western Australia, South Australia and Victoria, they are also evident in the illustrations of Verco and Cotton (1931).

REMARKS: Specimens of *Sepioteuthis australis* examined from Australia and New Zealand match closely with previous descriptions of *S. australis* by Quoy & Gaimard (1832, p. 77), Ferrusac & d'Orbigny (1834-48, p. 301). McCoy (1883, p. 27, Berry (1918, p. 249), Verco & Cotton (1928, p. 128) and descriptions of *S. bilineata* by Kirk (1884) and Dell (1952, p. 87). The similarity and probably conspecificity of *S. australis* from Australia and *S. bilineata* from New Zealand was pointed out by Adam (1939) and Dell (1952); however this is the first time that actual material from each locality has been compared. There do not appear to be any differences between Australian and New Zealand material examined which could substantiate separate species designations.

The name *Sepioteuthis bilineata* was introduced into New Zealand literature by Hutton (1880), a nomenclatural move which cannot be justified as his identification was based on the extremely poor type description of a specimen not originally from New Zealand, and which has been lost (Quoy & Gaimard 1832, p. 68). *Sepioteuthis bilineata* should be considered as a *nomen dubium* and the name *S. australis* applied to both Australian and New Zealand specimens.

The fragmented remnants of the beaks are all that remain of the type specimen of *Sepioteuthis australis*.

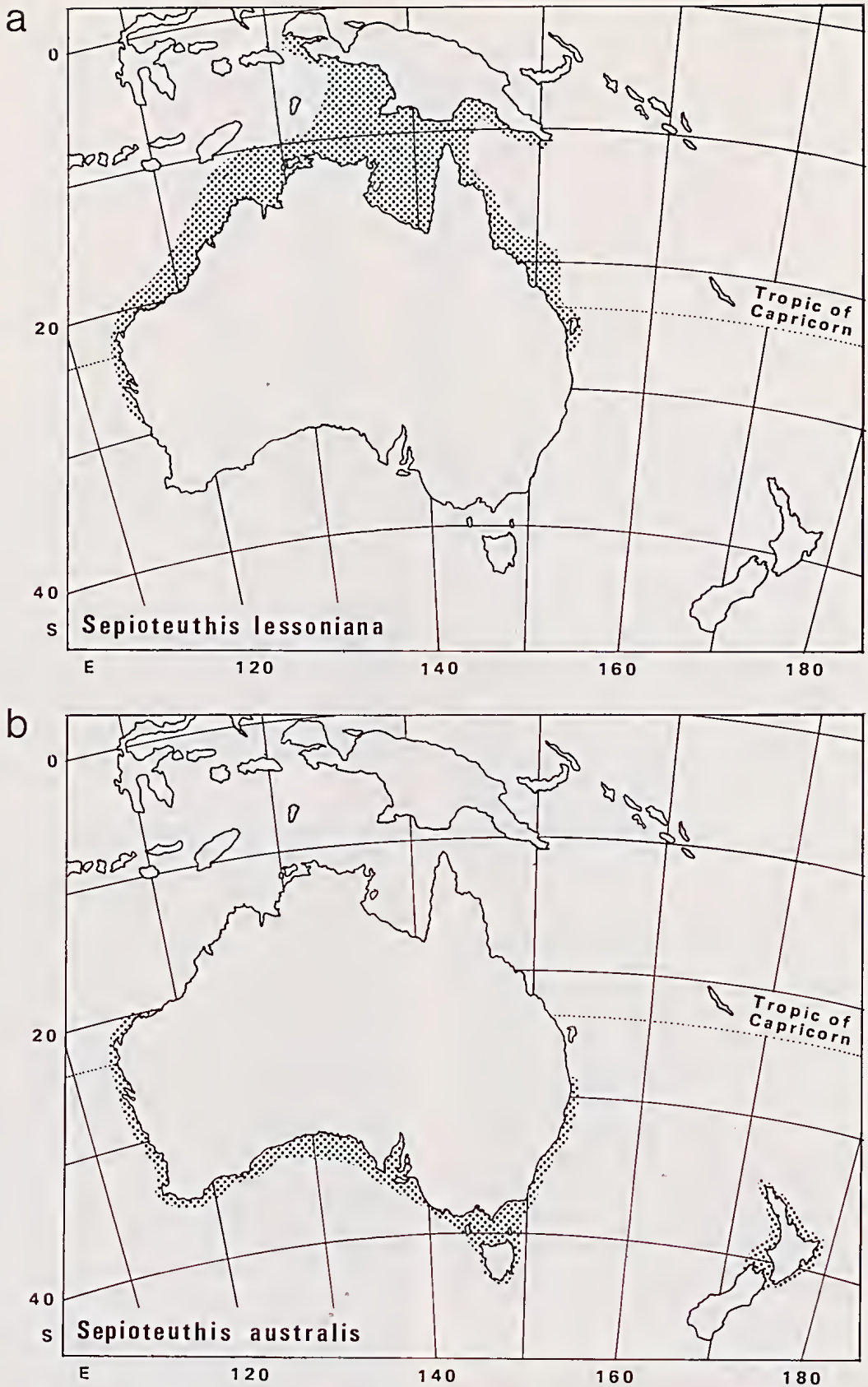


Fig. 8—a, distribution of *Sepioteuthis lessoniana* around Australia. b, distribution of *Sepioteuthis australis*.

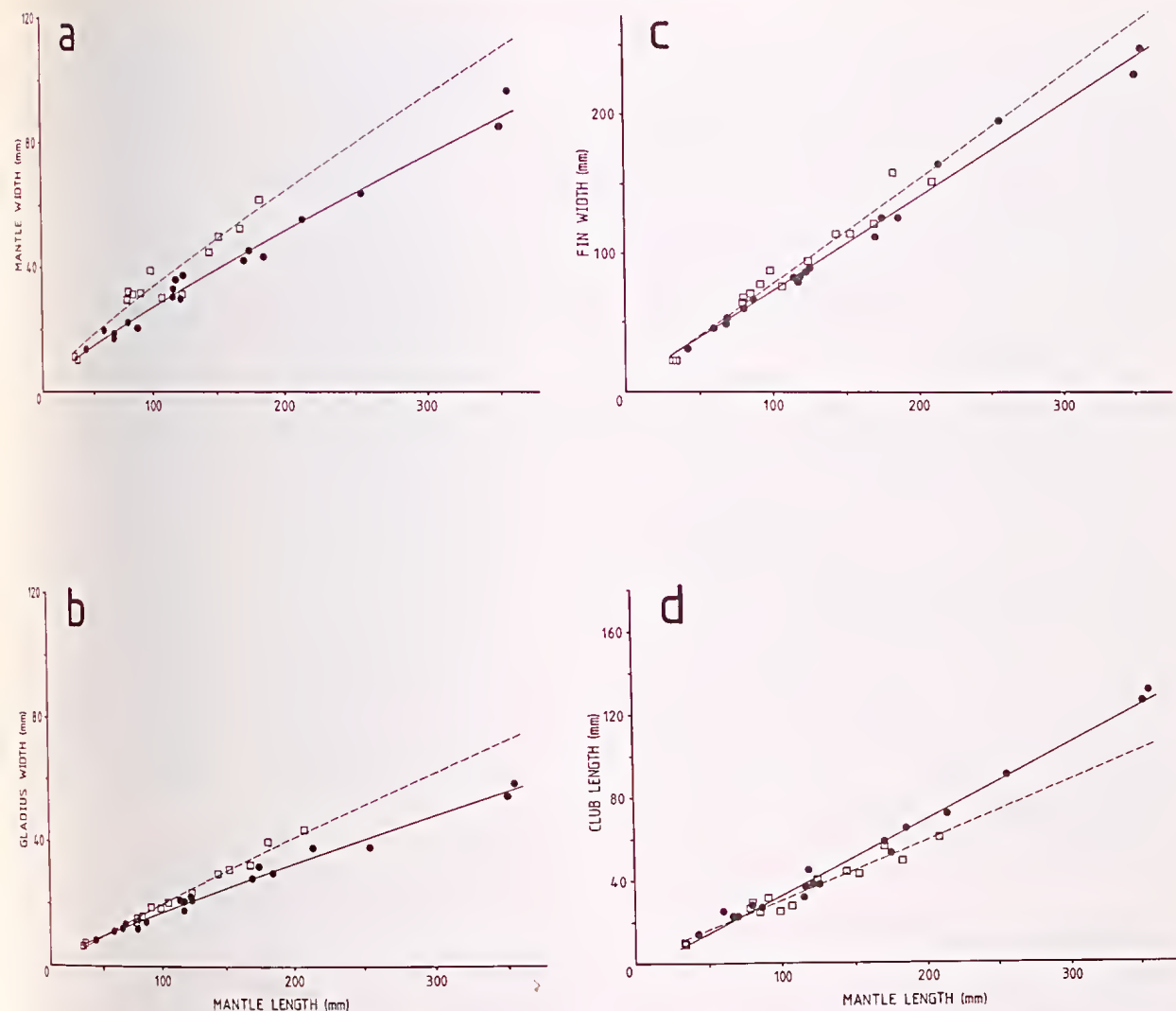


Fig. 9—Comparison of morphological parameters of *Sepioteuthis australis* from Australia and New Zealand. Australian sample—solid lines and solid dots. New Zealand sample—dashed lines and hollow squares. Regression data and comparisons of lines are given in Table 4.

These serve no useful taxonomic purpose; however, the complete type specimen was well described and illustrated by both the original authors and Férussac and d'Orbigny (1834-48).

Morphological differences which can be statistically detected between the Australian and New Zealand samples examined indicate that they are distinct populations. The New Zealand population is characterised by a relatively broader body, smaller tentacle clubs, smaller arm, and club sucker rings, and the spermatophore oral cement body lacking distinct shoulders. These differences are probably due to the isolating effect of the Tasman Sea on a neritic species.

DISCUSSION

Of the five species of *Sepioteuthis* recorded from Australia and New Zealand, only two are considered valid: *Sepioteuthis lessoniana* and *S. australis*.

Sepioteuthis lunulata of Brazier (1892) is a synonym of *S. lessoniana*. *Sepioteuthis mauritiana* described by Meyer (1909) from Albany, Western Australia is undoubtedly referable to *S. australis*. *Sepioteuthis mauritiana* is now known to be a synonym of *S. lessoniana*, but Meyer's illustration shows the fins of his specimen to be widest at their mid point. Further, Albany is far south of the recorded distribution of *S. lessoniana*, but well within the distribution of *S. australis*. This is in accordance with the opinion of Adam (1939, p. 28) as to the identity of Meyer's specimens. *Sepioteuthis bilineata* was poorly described from a single specimen from Western Port; no measurements were given and the poor illustration was evidently made from a quick sketch of a live animal. The inadequacy of the type illustration has since attracted comment by both Férussac and d'Orbigny (1834-48, p. 302) and Adam (1939, p. 30). The specimen was reported lost by the authors

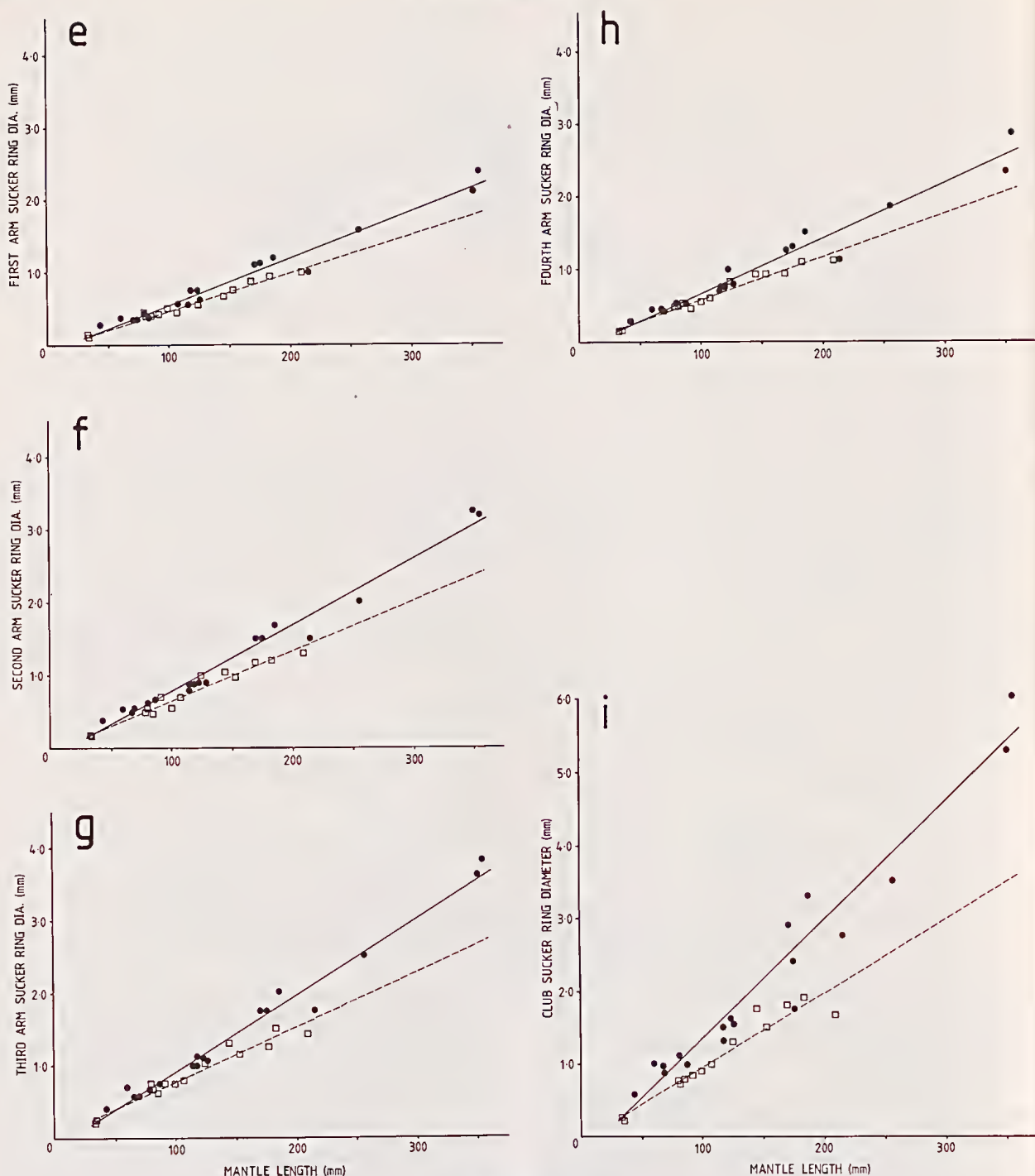


Fig. 9—(continued)

without any further information being available (Quoy & Gaimard 1832, p. 68). Dell (1952), based on Hutton's (1880) identification of the New Zealand species of *Sepioteuthis* as *S. bilineata*, submerged the name *S. australis* into synonymy with *S. bilineata*. This is impossible to justify in the absence of an adequate type description or type specimen of *S. bilineata*. Prior to

Dell, Adam (1939, p. 30) had already suggested *S. bilineata* to be a *nomen dubium*—'comme le *Sepioteuthis bilineata* est très mal connu et que le type a été perdu (selon les auteurs), tandis que le dessin original est très douteux, je ne crois pas pouvoir l'accepter'.

The New Zealand species of *Sepioteuthis* can be positively identified as *S. australis*, the validity of which



Fig. 10—*Sepioteuthis australis* Quoy & Gaimard. Geographic variation in spermatophore cement bodies from Australia and New Zealand. a, NMVF30876, 214 mm ML, S.E. Australia. b, NMVF31752, 250 mm ML, New Zealand.

species may be established beyond doubt due to the adequate type description and subsequent description and illustration of the type specimen by Ferrusac and d'Orbigny (1834-48). The validity of *S. bilineata* however, cannot be established with any degree of certainty and we therefore agree with Adam that *S. bilineata* is a *nomen dubium* and that the species of *Sepioteuthis* from southern Australia and New Zealand is *S. australis*.

ACKNOWLEDGEMENTS

We wish to thank the following individuals and institutions who made material available for study either as gifts or loans: M. Dunning, Division of Fisheries Research, CSIRO; Tasmanian Fisheries Development Authority; Victorian Department of Fisheries and Wildlife; M. Potter, Queensland Fisheries Service; H. Smith, South Australian Fisheries; R. Mattlin, Fisheries Research Division of New Zealand; Department of Zoology, University of Melbourne; S. Slack-Smith, Western Australian Museum; F. Climo, National Museum of New Zealand; J. Knudsen, Zoologisk Museum, University of Copenhagen; and P. Bouchet, Museum National d'Histoire Naturelle, Paris.

Sepioteuthis lessoniana from the Philippines was col-

lected by C.C.L. on the 1979 'Alpha Helix' expedition, sponsored by the National Science Foundation. Many thanks to John Arnold, University of Hawaii for his invitation to participate in the cruise. We are grateful to National Taiwan University and the captain and crew of the research vessel 'Hai Kung' who generously provided the opportunity to collect much valuable material. The financial support provided by A.B.R.S. to study Australian loliginids is gratefully acknowledged. Margaret Blackburn provided the illustrations and Lyn Anderson and Heather Martin typed the manuscript, for which we are indebted.

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APPENDIX 2 continued

	NMV F27004	NMV F31567	NMV F30852	NMNZ M74110	NMV F30241	NMNZ M5655	NMV F30851	NMV F31573	NMNZ M74106	NMV F30868	NMNZ M74106	NMNZ M74107	NMV F31574	NMV F30873	NMNZ M74117	NMV F31574	NMV F30876
Sex	M	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F
ML	355	43	69	80	80	85	116	118	124	125	144	153	170	175	183	186	256
VML	318	41	56	72	67	78	97	105	114	112	130	125	149	151	164	167	221
MW	96	14	18	32	22	31	31	36	36	37	43	50	42	45	62	43	63
HL	67	9	17	22	18	17	23	29	26	29	29	32	40	32	41	38	58
HW	68	14	20	27	22	25	35	28	31	33	36	34	43	39	42	43	64
FL	320	36	61	70	72	73	104	107	113	120	130	132	151	158	167	175	225
FW	250	31	51	69	61	71	82	73	95	99	115	115	112	126	160	127	197
AL _I	108	10	15	23	20	18	28	32	30	29	36	34	39	44	44	48	63
AL _{II}	132	14	22	31	29	28	36	48	42	41	51	52	55	57	60	68	88
AL _{III}	153	18	28	38	36	39	46	53	51	49	61	62	66	67	70	80	97
AL _{IV}	134	18	28	39	37	37	47	52	48	48	53	56	70	65	67	76	102
HA	145																
HC	27																
TL	440	38	50	102	65	90	75	173	129	94	98	99	158	150	128	162	262
CL	131	14	23	29	28	25	32	45	40	38	44	43	59	53	50	65	90
AS _I	2.4	0.3	0.4	0.4	0.4	0.4	0.6	0.8	0.6	0.6	0.7	0.7	1.1	1.1	1.0	1.2	1.6
AS _{II}	3.2	0.4	0.6	0.6	0.6	0.5	0.8	0.9	1.0	0.9	1.1	1.0	1.5	1.5	1.2	1.7	2.0
AS _{III}	3.8	0.4	0.6	0.8	0.7	0.6	1.0	1.1	1.1	1.1	1.3	1.2	1.8	1.8	1.5	2.0	2.5
AS _{IV}	2.8	0.3	0.4	0.5	0.5	0.5	0.7	0.8	0.8	0.8	0.9	0.9	1.3	1.3	1.1	1.5	1.9
CS	6.1	0.6	0.8	0.8	1.1	0.8	1.5	1.8	1.3	1.6	1.8	1.5	2.9	2.4	1.9	3.3	3.5
GW	59	8	13	16	12	16	22	21	24	22	29	31	28	32	40	30	38
RL	66	10	13	14	15		22	22	22	22	28	26	30	31	40	30	46
RW	18	2	3	5	4		6	6	7	7	9	8	10	10	12	11	14
SL	23																
NL		3	7	7	8	10		21	16	13	26	46	19	13	56	22	90

APPENDIX 3

MEASUREMENTS (IN MM) OF UPPER AND LOWER BEAKS OF 10 SPECIMENS OF *Sepioteuthis lessoniona* FROM AUSTRALIAN WATERS

	NMV F31551	NMV F31549	NMV F31552	NMV F31547	NMV F31548	NMV F31576	NMV F31556	NMV F31611	NMV F31546	NMV F31557
Sex	F	M	M	F	M	M	F	M	F	M
ML	85	104	118	132	172	217	218	220	250	356
Upper Beak										
ROL	1.4	2.4	2.7	3.0	3.2	3.9	4.1	4.0	5.1	7.7
ROW	1.6	2.4	2.7	2.7	3.3	3.5	3.8	4.1	4.6	6.7
WL	3.2	3.8	3.8	4.2	6.5	7.2	9.4	9.2	9.1	14.5
HdL	8.0	11.0	10.5	11.8	15.0	18.5	21.2	18.5	20.6	28.5
LWL	10.4	13.2	14.0	15.1	20.8	24.3	28.0		27.2	40.3
Lower Beak										
ROL	2.1	2.5	2.6	2.7	3.0	3.9	4.3	4.3	5.1	6.9
ROW	2.0	2.5	2.9	3.0	3.3	4.6	5.0	4.6	6.3	7.0
WL	5.3	6.6	7.2	7.6	10.5	12.5	16.0	12.4	14.7	23.7
BL	8.0	9.2	10.5	11.0	14.7	18.5	18.6	18.7	20.5	28.0
D	6.7	7.4	7.3	7.7	11.0	12.7	17.0	12.7	14.0	20.6
HdL	2.9	3.5	3.6	4.3	5.7	7.1	8.0	6.6	7.4	11.4
CrL	6.6	8.5	9.0	9.7	12.9	15.5	17.5	15.0	17.7	25.5
LWL	8.0	10.7	10.4	11.2	14.4	17.6	19.6	17.7	20.0	28.3

APPENDIX 4

MEASUREMENTS (IN MM) OF UPPER AND LOWER BEAKS OF 14 SPECIMENS OF *Sepioteuthis australis* FROM AUSTRALIAN AND NEW ZEALAND WATERS

	NNNZ M21933	NMV F31567	NMV F31572	NNNZ M74110	NMV F30868	NNNZ M11321	NNNZ M9829	NMV F30868	NNNZ M74106	NNNZ M74106	NMV F30873	NMV F31574	NMV F30876	NMV F27004
Sex	M	F	M	F	M	M	M	M	F	F	M	F	M	M
ML	34	43	68	80	87	99	107	117	124	144	175	186	214	355
Upper Beak														
ROL	0.6	0.7	1.1	1.4	1.1	1.5	2.0	2.3	2.5	2.1	3.0	3.8	3.7	5.4
ROW	0.6	0.8	1.1	1.5	1.1	1.2	1.7	2.0	1.9	2.4	3.0	3.2	4.0	5.6
WL	1.0	1.7	1.8	2.4	2.4	2.8	3.0	4.5	4.1	4.6	4.9	6.4	6.5	9.0
HdL	2.7	3.9	5.2	6.8	6.9	8.7	8.5	9.6	10.7	12.0	15.3	15.2	15.5	23.8
LWL	2.7	3.9	4.8	6.0	6.7	7.8	6.5	9.0		11.3	15.0	16.2	14.0	24.6
Lower Beak														
ROL	0.5	0.8	1.0	1.4	1.1	1.3	1.8	2.2	2.5	2.3	3.1	3.7	4.0	6.6
ROW	0.6	0.8	1.1	1.7	1.1	1.5	1.7	2.0	2.5	2.4	3.4	3.7	4.0	7.0
WL	1.7	2.8	3.2	4.5	4.4	5.3	6.0	6.5	6.9	7.8	10.4	9.8	12.0	16.1
BL	2.5	3.8	4.9	6.7	6.7	7.8	7.2	8.6	10.7	12.0	14.4	15.0	13.5	21.0
D	1.6	3.0	4.0	5.3	5.2	4.8	5.5	8.0	7.0	7.3	11.0	11.2	11.7	19.2
HdL	1.0	1.4	1.7	2.3	2.2	3.3	3.0	4.1	4.1	4.6	5.3	6.0	5.6	7.4
CrL	2.2	3.1	4.3	5.6	4.8	6.2	5.8	7.8	8.2	10.0	13.0	13.0	12.4	19.0
LWL	2.6	3.7	5.1	6.6	6.8	7.8	7.0	9.5	11.0	11.2	14.3	15.5	14.0	22.0

APPENDIX 5

MATERIALS EXAMINED: *S. lessoniana*

No.	Sex	ML (mm)	Reg. No.	Location	Date	Depth (m)
1	M	104	NMV F31549	16°31'S, 145°43'E	7-V-1981	31
1	M	110	NMV F31554	14°10'S, 124°26'E- 14°09'S, 124°29'E	26-III-1981	93-95
1	M	118	NMV F31552	16°40'S, 145°39'E	7-V-1981	13-18
1	M	155	NMV F31555	19°30'-20°10'E, 155°50'-177°20'E	X1-1981	45-75
3	M	157-208	NMV F31553	20°10'S, 116°04'E- 20°10'S, 116°08'E	9-III-1981	60
1	M	172	NMV F31548	18°05'S, 121°47'E- 18°01'S, 121°48'E	26-V-1979	40-42
2	M	196-217	NMV F31576	21°21'S, 114°44'E- 21°19'S, 114°40'E	4-V-1979	82-98
2	M	220-270	NMV F31611	27°12'S, 153°05'E	12-IX-1980	
1	M	356	NMV F31557	23°55'S, 152°24'E	1-VII-1980	
1	F	85	NMV F31551	14°02'S, 124°36'E- 13°59'S, 124°36'E	23-III-1981	86
1	F	95	NMV F31550	20°14'S, 177°12'E- 20°14'S, 177°15'E	2-VI-1981	39-40
1	F	132	NMV F31547	12°18'S, 124°04'E- 12°19'S, 124°06'E	31-III-1981	80-91
1	F	155	NMV F31575	13°14'S, 125°07'E- 13°13'S, 125°05'E	30-III-1981	77
2	F	218-224	NMV F31556	27°10'S, 153°03'E	7-X-1980	
1	F	250	NMV F31546	20°00'S, 116°05'E- 20°03'S, 116°08'E	9-III-1981	62-66
10	M	72-259	NMV F31764	9°52'N, 123°09'E	X1-1979	
11	F	62-197				
1	M	112	ZMC	Nhatrang Fishmarket, Vietnam	7-X-1959	

APPENDIX 6

MATERIALS EXAMINED: *S. australis*

No.	Sex	ML (mm)	Reg. No.	Location	Date	Depth (m)
2	M	33-34	NMNZ M21933	35°13'S, 174°04'E	III-1967	
2	M	56-56	NMV F31331	27°40'S, 153°29'E	6-XI-1981	32
1	F	48				
1	M	60	NMV F24447	38°09'S, 144°23'E		
1	M	68	NMV F31572	40°00'S, 144°21'E	2-II-1981	47
				40°00'S, 144°26'E		
1	M	79	NMNZ M74110	41°17'S, 174°54'E	1-XII-1960	
1	F	80				
2	M	87-117	NMV F30868	40°31'S, 145°04'E	3-XI-1980	29
1	F	125				
1	M	91	NMNZ M11174	41°19'S, 174°48'E	10-IV-1957	
1	M	99	NMNZ M13321	41°16'S, 174°48'E	I-1959	
1	M	107	NMNZ M9829	41°19'S, 174°53'E	16-V-1959	7
2	M	114-208	WAM 785-81	c 20°S, 116°E		77-84
1	M	123				
1	F	116	NMV F30851	38°21'S, 145°13'E	25-III-1981	
1	M	169	NMNZ M17891	36°19'S, 175°29'E	1962	
1	M	175	NMV F30873	39°56'S, 144°48'E	3-II-1981	49
				39°54'S, 144°48'E		
1	M	209	NMNZ M74108	41°15'S, 174°50'E	XI-1952	
1	M	214				
1	F	256	NMV F30876	40°38'S, 145°23'E	4-XI-1980	36
4	M	250-300*	NMV F31752	c 41°S, 175°E	21/28-VII-1982	
1	M	300*	NMV F31753	38°32'S, 145°21'E	28-XI-1982	6
1	M	342	NMV F31756	38°32'S, 145°21'E	28-XI-1982	6
2	M	350-355	NMV F27004	38°17'S, 144°40'E	1882	
2	M	362-382	NMV F31755	Melbourne Fish Market	13-IX-1888	
1	F	43	NMV F31567	39°03'S, 146°29'E	10-II-1982	13
1	F	69	NMV F30852	Western Port Bay, Vic.	2-V-1967	
1	F	80	NMV F30241	38°21'S, 145°13'E	8-VI-1974	
1	F	85	NMNZ M5655	Wellington Hbr, N.Z.		
1	F	118	NMV F31573	34°55'S, 137°48'E	24-IX-1979	31
2	F	124-144	NMNZ M74106	34°59'S, 173°57'E	VII-1953	
1	F	153	NMNZ M74107	34°59'S, 173°57'E	I-1954	
2	F	170-186	NMV F31574	38°47'S, 146°45'E?	13-XI-1959	20
1	F	183	NMNZ M74117	35°14'S, 174°08'E	1960	
		268-280	NMV F31754	40°31'S, 145°04'E	3-XI-1980	29

* Indicates reproductive organs only examined.

PALAEOZOIC ACID VOLCANISM IN VICTORIA

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'... something of the nature of a cataclysm of lavas, mainly acid, must have overwhelmed Victoria in Upper Devonian times' (E. S. Hills, 1932)

ABSTRACT: Although the limits of the major belts of 'dacites' in central Victoria, and acid-intermediate rocks elsewhere were established by the early 1900s, it wasn't until E. S. Hills commenced work in the Cathedral Range area in 1928 that the age relationships were clarified. Following his discovery of a Late Devonian fish fauna between the basement sediments and the main volcanic units in the Cerberean Cauldron, Hills worked extensively in the region for the next 30 years, eventually concluding that a mechanism of cauldron subsidence enabled the eruption and emplacement of the acid volcanic rocks in most of the Central Victorian complexes. Since the 1960s, debate has concentrated on the role of ash flows, as distinct from lavas, in the emplacement of large volumes of acid volcanic rocks. However, there was no general discussion, let alone agreement, on the Victorian occurrences until the 1970s.

This paper reviews the contribution made by early geologists, culminating in the work of Skeats and Hills, towards the current knowledge of acid volcanism in Victoria. The development of the concept of ash-flows and their association with large-scale subsidence complexes is discussed. The features of the main belts of acid-intermediate rocks in Victoria are outlined, their chemical and mineralogical characteristics summarised and a possible model for the origin of the magmas presented.

In 1980, Mt. St. Helens, Washington, provided a yardstick for the awesome power of explosive volcanism. However, even this eruption and its devastating effects pale into geological insignificance when compared to volcanic activity which occurred in the Victorian region during the Late Devonian. Here, over a period possibly as short as 3-5 million years, some of the most spectacular eruptions and simultaneous crustal displacements ever to affect a relatively small area of the earth's crust took place. And the evidence for these events is remarkably well preserved in a number of subsidence complexes in Central Victoria (Fig. 1).

HISTORICAL SUMMARY

Edwin Sherbon Hills may well have been drawn to the Cathedral Range area, 80 km north east of Melbourne, in early 1928 as much by its scenic and geomorphological qualities as by the suggestion from Professor E. S. Skeats that here the relationship between the Cathedral Beds (then believed to be Late Devonian or Early Carboniferous) and the supposed Early Devonian 'dacites' may be revealed. Skeats had maintained an interest in the 'dacite' problem and was instrumental in establishing a degree of order to the diverse geological data accumulated since the 1850s (Skeats 1909, 1910).

As early as 1854, Selwyn had regarded the 'Palaeozoic Traps' of the Melbourne region as intrusive on the basis of what seemed to be gradational contacts with granitic rocks. This interpretation (e.g. Murray 1895) persisted until the early 1900s; for example, extensive areas of rocks now known to be volcanic units were shown as granite on the 1902 Geological Map of Victoria (8 miles to inch). In the east of the State, an extensive belt of acid volcanic rocks, the 'Snowy River

Porphyries' had been broadly delineated by Howitt (1876) with subsequent contributions from Murray (1877, 1887), Whitelaw (1899) and Ferguson (1899). Kitson (1899) correlated acid volcanic rocks near Whitfield (now the Tolmie Highlands Complex) with the Snowy River Porphyries. In the first detailed investigation of a Central Victorian volcanic complex, Gregory (1902) concluded that the Mt Macedon 'dacite' was volcanic and assigned an age between early Mesozoic and early Cainozoic. Petrographic and mineralogical similarities prompted Gregory to conclude that the Macedon 'dacites' were related to those known from the Dandenongs, Healesville and the Cerberean Ranges. Skeats and Summers (1912) reinforced Gregory's claim for such a relationship, but overturned some of his other conclusions. In western Victoria, Dennant (1893) partially described the occurrence of 'quartz porphyries' in the Hamilton-Cavendish-Balmoral area. The acid series of volcanic rocks ('felsites', 'quartz felsites') in the Mt. Wellington area of Gippsland was described by Howitt (in Murray 1877, 1891).

So, by the early 1900s, most of the acid volcanic belts in Victoria had at least been delineated, even if petrographic, geochemical and stratigraphic information was virtually non-existent. However, major problems remained unresolved; the general relationship between the 'dacites' and granodiorites of central Victoria was uncertain, and the age of the complexes themselves was subject to debate.

Credit for the first broad review of these problems concerning acid volcanism in Victoria should go to Skeats (1909) who drew a distinction, mainly on petrographic and geographic grounds, between the 'Snowy River Porphyries' and the 'Dacite and Quartz-Porphyrite Series' of central Victoria. Both series he

Fig. 1 — Map showing distribution of the main belts of Palaeozoic acid-intermediate volcanic rocks in Victoria. Cambrian greenstone belts are shown in black.
 1, Rocklands Rhyolite. 2, Macedon Complex. 3, Dandenong Complex. 4, Marysville Complex. 5, Violet Town Volcanics. 6, Tolmie Highlands Complex. 7, Wellington Rhyolite. 8, Mitta Mitta Volcanics. 9, Jemba Rhyolite. 10, Thorkidaan Volcanics. 11, Snowy River Volcanics.



placed in the Early Devonian. This age for the Snowy River Porphyries was reasonably well established by palaeontological controls (Skeats 1909, Howitt 1890), but the argument for a similar age for the central Victorian complexes was somewhat circular. The volcanic rocks were clearly younger than the 'Silurian' and Ordovician basement sediments, the sequence in the Tolmie and Toombullup Ranges was overlain by Carboniferous sediments (Summers 1908) and the granodiorites, which were generally accepted as Devonian, were slightly younger than the 'dacites', based on contact relationships in the Dandenongs and at Mt. Macedon.

Skeats had drawn on widespread evidence to establish the relationship between 'dacite' and granodiorite. Even so, some ambiguity persisted over the nature of the dacite itself, as Skeats admitted 'I think a good deal of the Marysville dacite must be regarded as intrusive rather than effusive'. Given the very coarse-grained recrystallisation textures exhibited by some of the units, such a view may be excused in the absence of detailed stratigraphic information at that time. Somewhat prophetically, Skeats observed that the 'dacites' in the Dandenong and Strathbogie Ranges and at Narbethong and Marysville, passed, without sharp junction, into 'quartz porphyries' or 'quartz porphyrites'. The significance escaped Skeats at the time, but the mineralogical gradation between major volcanic

units was later to prove important in enabling Hills to establish the age of the 'dacites'.

THE ROLE OF E. S. HILLS

Hills essentially set out in 1928 to solve an age relationship problem. This he accomplished quickly, showing that a strong unconformity existed between the overlying volcanic rocks and the Cathedral Beds, which he placed high in the Late Silurian.

Discovering that a series of acid lavas, basalts and sediments occurred on the slopes of the Blue Range, immediately east of Cathedral Range, he mapped them for a strike distance of about 10 km and established the first generalised sequence (Table 1) in what was to become known as the Cerberean Cauldron. Hills then found a fossiliferous sequence of lacustrine sandstones and shales, between the basal conglomerate to the volcanic sequence and the main rhyolite (Rhyolite α) forming the summit of the Blue Range near Taggerty. These 'Taggerty fish beds' established a Late Devonian age which enabled Hills to confidently state that the volcanic rocks in the Cathedral district were Late Devonian (Hills 1929a). Hills was the first to break free of the early attempts to 'pigeon hole' all the volcanic rocks into the Early Devonian. However, the argument for extensive Late Devonian volcanism in Victoria required a further step, namely determination of the relationship between the volcanic sequence at Taggerty and the more

TABLE 1
HISTORICAL DEVELOPMENT OF THE CORRELATION OF SEQUENCES WITHIN THE CERBERIAN AND ACHERON CAULDRONS

[illegible]

widespread 'dacites'. The sequence of volcanic rocks, tuffs and sediments at Taggerty was actually the second piece of a jigsaw puzzle which was to take nearly 55 years to complete. In 1915, Junner had mapped part of a similar volcanic sequence near Narbethong, nearly 30 km south of Taggerty. In the Marysville-Cumberland region, east of Narbethong, Hills clearly showed that rhyodacite ('dacite') overlay the main rhyolite ('nevadite') which he traced along strike and confirmed as his Rhyolite α at Taggerty (Hills 1929b, 1932). It was however, impossible to map a boundary between the two rock types as they merged through continuous vertical mineralogical variation, a feature alluded to previously by Skeats. This continuity could only mean that no great age difference existed between the two and hence the Marysville 'dacites' must have been Late Devonian.

Hills then argued, as others before him had done, that the close similarity between the Marysville 'dacites' and those at Macedon, Lilydale (Dandenong Ranges), the Strathbogies and Tolmie (Tolmie Highlands) was good evidence for an identical age, now shown to be Late Devonian, for all. This prediction has since been confirmed by radiometric dating techniques (McDougall *et al.* 1966, Richards & Singleton 1981).

Perhaps surprisingly, nearly thirty years separate Hills' 1932 paper and his 1959 discussion on the relationships between acid magmatism and crustal fracturing in southeastern Australia. Hills' treatment of the topic was to discuss individual complexes in the region, with the greatest prominence being given to the Cerberean Cauldron. He did however, examine the structure of the Dandenong Ranges Complex in 1941, but made no reference to the mechanism of emplacement. It is clear that Hills spent the interval of twenty-seven years fruitfully, not only by encouraging others to investigate similar complexes in central Victoria (e.g. D. A. White in the Strathbogies, D. E. Thomas at Eildon), but also by continuing his own tasks of mapping the volcanic sequence in the Cerberean Ranges and preparing a monograph. He also wrote two short papers, one on myrmekite (Hills, 1933), the other on oscillatory zoning in plagioclase (Hills, 1936), both based on observations made on feldspars in the 'nevadite-dacite' sequence at Marysville.

It was not until after his 1935 review of the Victorian Devonian (Hills 1935) that Hills became aware of the possibility that the volcanic sequence between Taggerty and Marysville was part of a cauldron subsidence struc-

ture, with a surrounding ring dyke. During the 1940s and 1950s, Hills tested this hypothesis by mapping the whole Cerberean complex. Although most of this must have been at a reconnaissance level, particularly on the eastern side of the ranges (where Whitelaw, on an earlier (1913) unpublished map, had shown parts of the eastern ring dyke), it was sufficient to confirm his theory. A thick sequence of volcanic rocks, with a basin-like structure, covered an area of about 400 km², and was surrounded by a near-circular ring fracture, partly dyke-filled, with a diameter of 27 km.

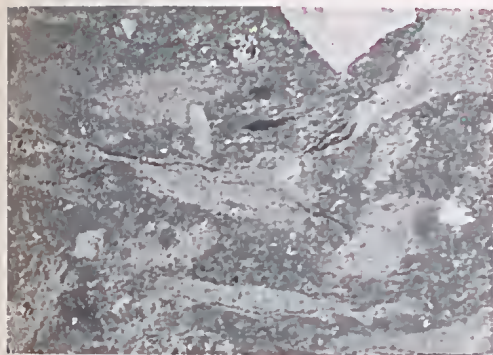
Hills also recognised the Acheron Cauldron to the south, which, together with the Cerberean and a belt of intrusive rocks to the west (the Black Range) formed the Marysville Igneous Complex. He also pointed out that the Marysville Complex was not the only cauldron subsidence in the region. Closely related complexes such as the Violet Town Volcanics were also bounded by near vertical fractures, although these tended to be polygonal, rather than arcuate or elliptical.

The monograph on the Marysville Igneous Complex, which Hills was preparing, has not been published. However, it was made available to D. E. Thomas, who quoted from the manuscript when preparing his 1947 report on the geology of the Eildon Dam site. M. Valiullah, a student at Melbourne University in the early 1960s, also had access to the monograph when undertaking a chemical and mineralogical study of the Central Victorian complexes (Valiullah 1964).

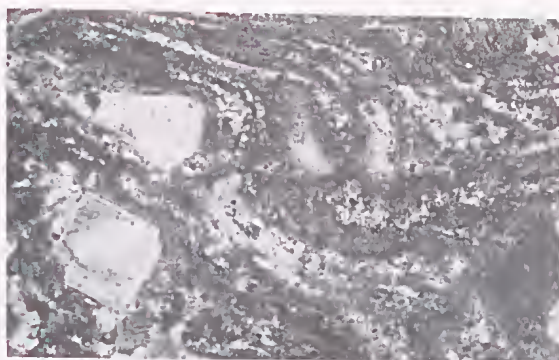
The 1960s saw the widespread application of K-Ar dating to stratigraphic problems in southeastern Australia. The Taggerty-Eildon sequence was ideal and, for a time, the Devonian-Carboniferous boundary was very closely identified with the uppermost rhyodacite in the Cerberean Cauldron (Evernden & Richards 1962, McDougall *et al.* 1966). Hills played a major advisory role in the application and interpretation of the radiometric data.

Thomas' map of the northernmost outcrops of the volcanic rocks in the Cerberean Cauldron was a classic piece of work and the famous Snobs Creek sequence is as significant for the interpretation of the structural history of the complex as the Taggerty fish bed sequence was for the stratigraphic correlation. The Snobs Creek sequence (Table 1) provided the base which enabled groups of honours students from the University of Melbourne to complete, in detail, the mapping begun by Hills some 40 years earlier (Birch *et al.* 1970, Dudley *et al.* 1971). Although he took no part in the field work

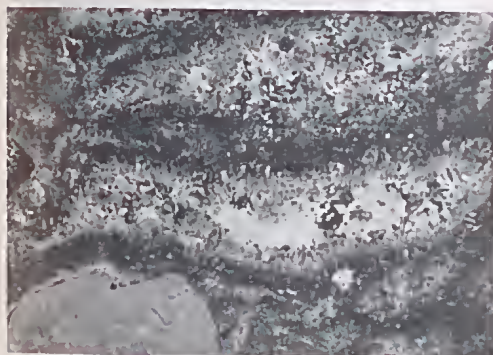
Figs 2-9—2, 3, photomicrographs of the base of the Rubicon Rhyolite in the Blue Hills, Taggerty, showing well developed eutaxitic texture. The contorted and flattened pumice fragments were interpreted as flow structure by Hills. 4, microspherulitic structure within flattened pumice fragments in the Rubicon Rhyolite from the Blue Range at Taggerty. These textures are a product of devitrification and vapour phase crystallisation. 5, 6, general texture within the 'fragmental toscanites', now rhyolites and rhyodacites of the Robleys Spur Formation. Note the fragmented phenocrysts in Fig. 5, and the andesite xenolith in Fig. 6. 7, vitroclastic texture (i.e. of flattened shards derived from shattered glass bubbles) well preserved in the Snobs Creek Rhyolite. 8, eutaxitic textures from the base of the Rubicon Rhyolite at Snobs Creek, Eildon. 9, general texture within the Rubicon Rhyolite, higher in the sequence at Snobs Creek. Recrystallization has partially obscured the original eutaxitic textures. Note: Figs. 2-9. Field of view is 3.5 × 2.3 mm.



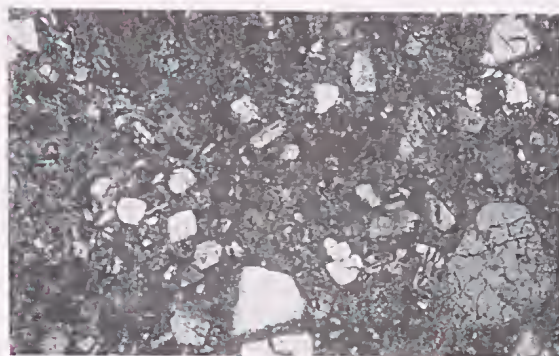
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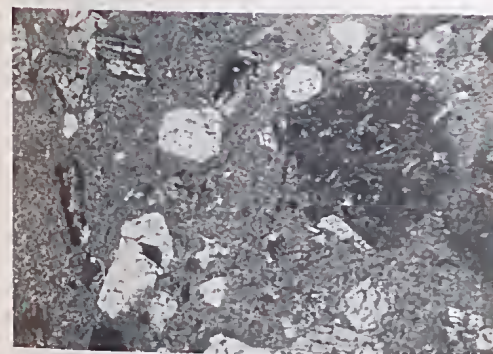
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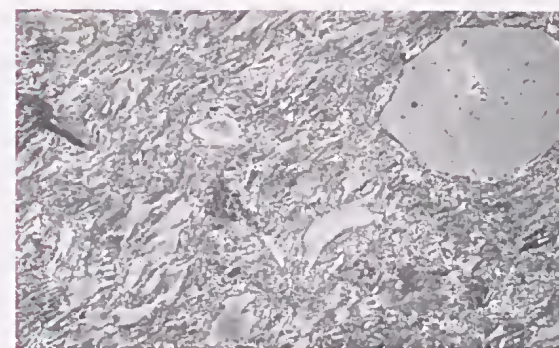
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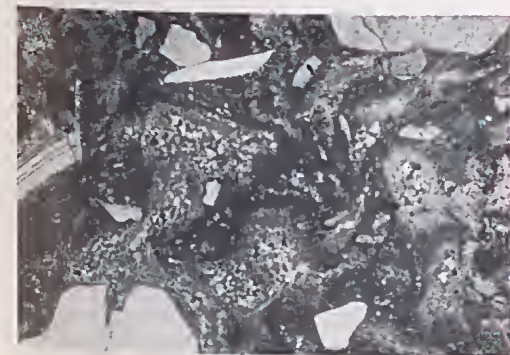
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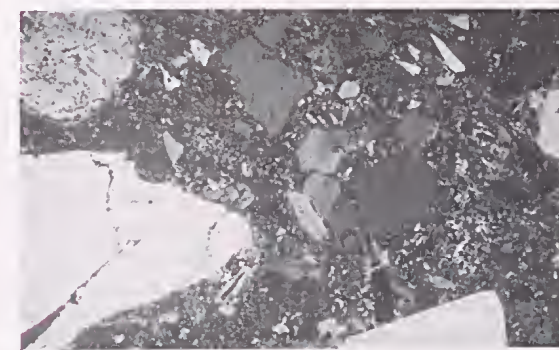
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8



9

during the 1970s it was Hills' influence which enabled the projects to be funded.

THE ASH-FLOW CONCEPT

EARLY INTERPRETATIONS IN VICTORIA

As already outlined, it was proving to be difficult enough for the early workers on the 'dacites' problem in Central Victoria to confirm the rocks had an extrusive origin without extending the debate to the mechanisms by which silicic volcanic rocks in general were emplaced. It was only when detailed petrographic studies of the 'dacites' were carried out that 'fluidal textures', clearly of volcanic origin, were recognised and described (Gregory 1902, Skeats & Summers 1912). The significance of these 'fluidal textures' naturally escaped even such an astute observer as Skeats, because over fifty years were to elapse before the concept of ash-flow emplacement influenced geological thought in Victoria.

Hills' work on the acid volcanic rocks at Taggerty involved quite detailed petrographic descriptions. In 1929, in Rhyolite α from Taggerty, he noted '*fluxion structure is developed only along the lower edge . . . Through the whole flow—but becoming more numerous towards the base, are xenoliths of sandstone and shale*'.

In describing microscopic features of this rhyolite, Hills noted that '*the groundmass is micro- to cryptocrystalline and always has well developed flow structure, the contorted lines curving around the phenocrysts of quartz and feldspar, which are not arranged linearly* (Figs 2 and 3). *Biotite crystals curve with the flow lines and wrap around the quartz and feldspar. On solidification, the groundmass was evidently a glass . . . Some bands are coarser than others . . . other bands are cryptocrystalline . . . occasional microspherulitic aggregates occur*' (Fig. 4).

Hills also described the highly fragmented nature of the phenocrysts and the microfluxion structure within the groundmass of Rhyolite β at Taggerty. These features of both rhyolites Hills ascribed to viscous flow and all the acid rocks were considered to be lavas rather than pyroclastics. Similarly the flow planes within the 'Lower' and 'Middle' Dacite units in the Dandenongs Complex were interpreted as bedding within lava flows (Hills 1941).

That Hills began to modify his views is apparent from references to his unpublished manuscript made by Thomas in 1947. Rhyolite β had been renamed the 'fragmental' toscanites (Table 1) in recognition of certain pyroclastic features they exhibited, such as the presence of shattered, but otherwise unaltered phenocrysts (Fig. 5) their well-stratified nature and the occurrence of xenoliths (Fig. 6). Strictly speaking, none of these features is exclusive to pyroclastic rocks, but Hills believed that the fragmental toscanites were erupted as *nuée ardentes*, coinciding with the initiation of the ring fracture. Their emplacement was followed immediately by the extrusion of the great 'nevadite-toscanite-dacite' 'lava' flows (now the Cerberean Volcanics). The suggestion of *nuée ardente* volcanism

was apparently as far as Hills was ever to go towards postulating an ash-flow or ignimbritic origin for any of the main acid volcanic units in the Cerberean Cauldron.

DEVELOPMENT OF THE ASH-FLOW CONCEPT

It is worthwhile setting these local interpretations in an international context. As Chapin and Elston (1979) point out, by 1942 the characteristic field and petrographic features of ash-flow tuffs had been documented worldwide and the relationship of ash-flow eruptions to cauldron collapse structures was well known. Yet the ability to recognise and interpret ash-flow tuffs remained the preserve of a small group of specialists until 1960 and their importance received scant recognition in major texts of the period.

Chapin and Elston advance two reasons for this neglect, namely: 1, the preoccupation amongst igneous petrologists with classification schemes, phase equilibria and differentiation studies; modes of emplacement were unimportant. 2, the great debators on the origin of 'granite' put on their blinkers when it came to large volumes of silicic volcanic rocks; volcanism (i.e. 'basalt') and plutonism (i.e. 'granite') were considered entirely unrelated.

During this period (1942-1960), Hills must have been developing his theories on the significance of acid volcanism in Victoria. Yet there is no published evidence, apart from the case of the 'fragmental toscanites' that Hills embraced the ash-flow theory. As early as 1932, he had acknowledged the problem of emplacing the huge volumes of magma in Victoria (up to 20 000 km² may have been covered to depths of 600-1200 m) by suggesting that fissure eruptions must have been dominant over central-type volcanism. Yet the associated problem, how to emplace widespread, sheet-like, roughly flat-lying deposits, showing continuous and relatively uniform mineralogical zonation, by a process of viscous flow, needed some discussion.

It is intriguing to speculate whether the two factors advanced by Chapin and Elston diverted Hills from taking part in the ash-flow debate. Armed as he was with the detailed stratigraphic, petrographic and structural evidence which he had accumulated in Victoria, he was in a position to profoundly influence the discussion.

SUBSEQUENT INTERPRETATION IN VICTORIA

In the early 1960s, the ash-flow theory gained widespread acceptability and respectability as a direct result of the landmark papers by Smith (1960a, 1960b) and by Ross and Smith (1961). These three papers were so thorough in their treatment of the field and petrographic characteristics of ash-flow tuffs that geologists began to fall over each other discovering new examples. Only a very small ripple, however, was felt in Victoria. White (1963) used Ross and Smith's criteria to suggest that the thin basal rhyolite of the Violet Town Volcanics, which he had studied in 1954, was a welded ash-flow. Remnant primary eutaxitic and vitroclastic textures in the chilled base of the overlying highly-recrystallized 'dacite' also pointed to an ash-flow origin

for this unit and on this basis. White extended this emplacement mechanism to the main volcanic units in other complexes, including the Snowy River Volcanics.

Brown (1963) disputed White's contention mainly on the basis of thickness/breadth ratios (which he considered, at values up to 1:10, as being too high for ash-flow sheets). Brown did, however, in 1962, reinterpret the Hollands Creek Rhyodacite (a unit underlying the volcanic rocks in the Tolmie Highlands Complex and which he had named in 1961) as an ignimbrite. Although these relatively brief notes generated no further discussion, White and Brown must take credit for undertaking a reinterpretation of their earlier work in the light of prevailing developments in ash-flow theory.

In 1968, M. D. Leggo described 'recrystallized ignimbrites' from the base of the Jemba Rhyolite but did not suggest the entire rhyolitic unit was an ash-flow deposit. The major reinterpretation took place in the early 1970s, when a re-examination of the 'fluxion structure' observed by Hills at the base of the main rhyolite (Rhyolite α , 'Nevadite', Rubicon Rhyolite) in the Cerberean Cauldron revealed it as remnant eutaxitic and vitroclastic textures typical of welded ash-flow tuffs (Birch *et al.* 1970). Recrystallisation, due mainly to the great thickness (and therefore retained heat) of the flow units, had obliterated primary textures from all but the thin basal zone (Birch 1978). All the major rhyolite and rhyodacite units in the sequence, from the Snobs Creek Volcanics upwards, showed characteristic features of welded ash-flows (Figs. 5-9).

Since then, more intensive study of the petrographic features of volcanic rocks in the Strathbogie and Tolmie Highlands Complexes (Clemens 1981, Birch 1978, 1975), the Jemba Rhyolite (Birch 1978) and the Dandenongs Complex (VandenBerg 1971) has demonstrated the universality of the ash-flow emplacement mechanism in Victoria.

Quite sophisticated studies on the major ash-flow deposits in the U.S.A. and New Zealand have since extended the knowledge of the emplacement mechanisms and the resulting textural, mineralogical and chemical variations (e.g. Sparks 1976, Sparks & Walker 1977, Sparks & Wilson 1976, Sparks *et al.* 1973, Christiansen 1979, Hildreth 1979, Wright *et al.* 1981). In many cases however, non or poorly welded ash-flow units were the objects of investigation and the application of the results to the densely welded Victorian examples is not necessarily practical nor valid.

GENERAL PATTERN OF ASH-FLOW AND CAULDRON SUBSIDENCE RELATIONSHIPS

The relationship between large collapse structures and silicic volcanism was first demonstrated by Williams (1941). Although this now has universal acceptance, there is still some disagreement over terminology relating to the structures themselves. Williams established the term 'caldera' for large, approximately circular volcanic depressions produced by 'engulfment'. The term 'cauldron' has been used for a wide range of structures and Smith and Bailey (1968) considered it ap-

propriate for all volcanic structures regardless of shape, size or depth of erosion. While 'caldera' is now widely acceptable in the U.S.A. and elsewhere, 'cauldron' is used more often in Australia, possibly due to the influence of Hills' 1959 discussion paper. However, there is no clear distinction between complexes described in the literature as calderas or cauldrons, and fundamentally the same mechanism probably gives rise to all such structures. The term 'cauldron subsidence', when applied to the central Victorian complexes, will be persevered in this paper, on the understanding that it is broadly synonymous with 'caldera'.

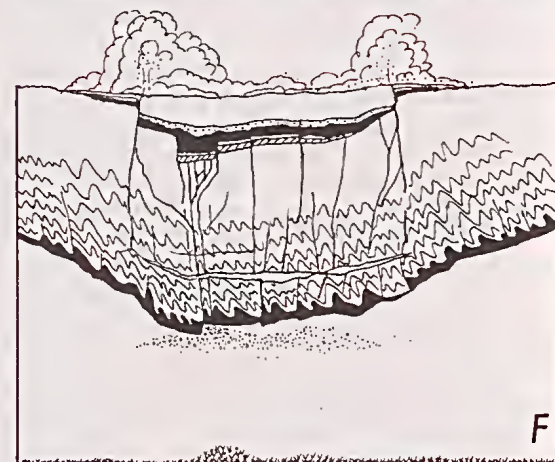
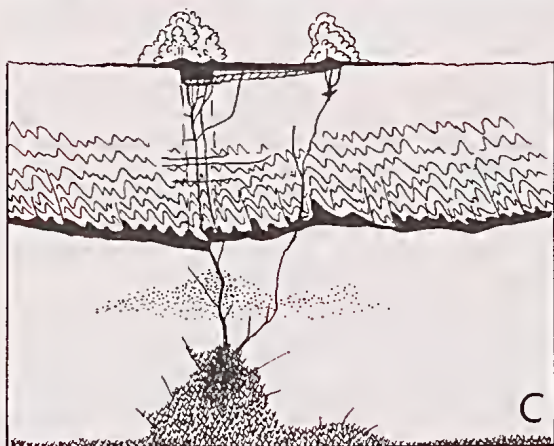
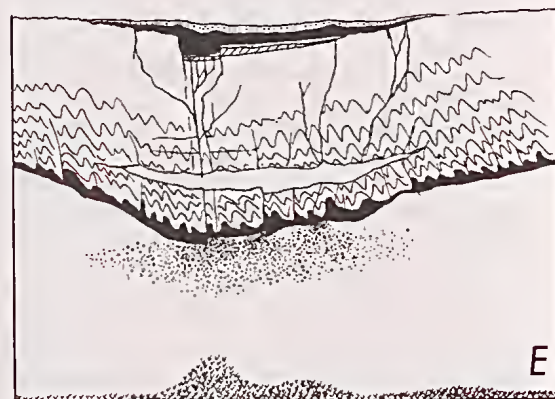
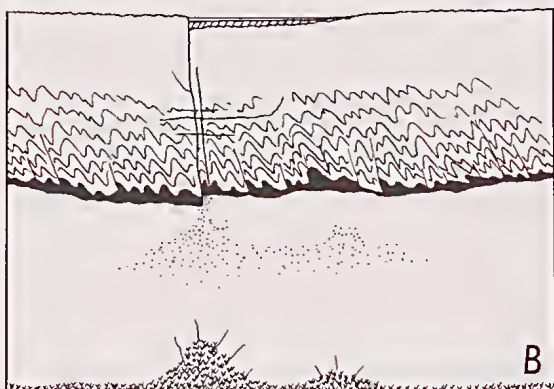
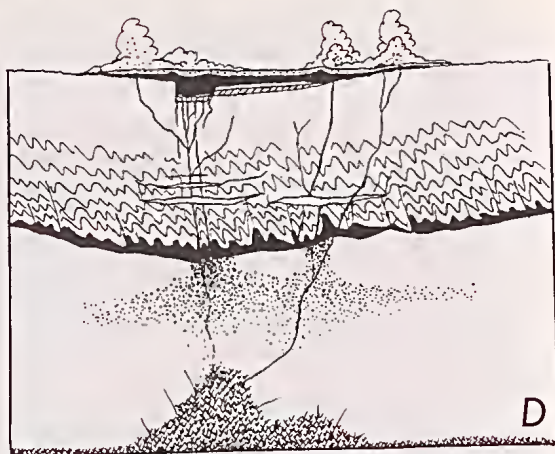
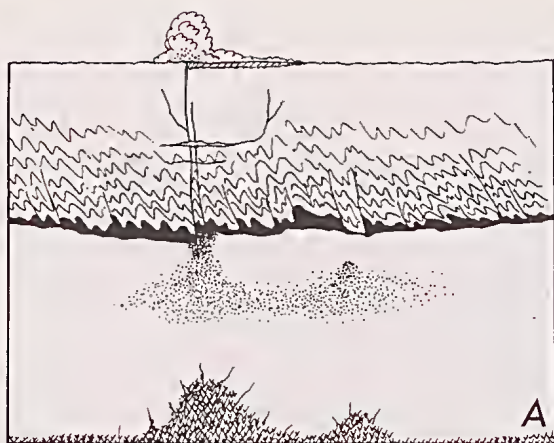
In framing a model, account must be taken of a diverse set of parameters. Scale is a useful initial discriminant. Ash-flow volumes of the order of 100 to 1000 km³ are characteristic of large epicontinental ring structures, and of the silicic volcanic eruptions associated with the large plutons of the circum-Pacific batholith complexes (Smith 1979). The central Victorian province fits into this latter category.

From the discussion papers of Smith (1979) and Christiansen (1979) a number of broad relationships may be defined, namely: 1, there is a positive correlation between the area of subsidence and the ash-flow eruption volume. 2, most large subsidence complexes show some degree of periodicity, with cyclic episodes of ash-flow eruption, occasionally with more basic lavas associated. A time scale of thousands to hundreds of thousands of years may be involved in a single cycle. 3, large ash-flow sheets show some degree of chemical and mineralogical variation inherited from the magma chamber. In general, they range from rhyolitic to dacitic or andesitic, reflecting a magma chamber becoming increasingly mafic with depth. This fractionation may have a number of origins. 4, most large-volume ash-flow sheets show an increase in phenocryst content upward in the sheet. The upper zone of phenocryst-poor magma within a crustal chamber is a low-temperature layer rich in volatile material; eruption inverts this zonation. 5, in large-volume silicic magmas, a maximum viscosity range above which ash-flows do not form appears to be in the region of 50% phenocryst content. 6, ash-flow sheets may represent both volatile oversaturated and volatile undersaturated magmas. In either case they represent the partial catastrophic evacuation of a shallow magma chamber from the top downwards.

THE DEVELOPMENT OF THE CERBEREAN CAULDRON MODEL

Hills' 1959 paper was a major contribution to the discussion on the mechanisms of 'cauldron subsidence'. There is little doubt that the Victorian region, and particularly the Cerberean Complex, is a key area in developing an understanding of the fundamental processes involved.

Based on the mapping of the Taggerty, Marysville-Cumberland and Eildon sequences within the Cerberean Complex, Thomas (1947), with the assistance of Hills, established the first model. It invoked progressive basining and continuous volcanism, with acid lavas and



pyroclastics interbedded with lacustrine sediments, prior to extrusion of widespread and generally overlapping basic lavas. In areas within the new, more developed basin, substantial lake deposits were ultimately represented by the Taggerty Fish Beds in the southwest, but marked by only thin tuffs in the Eildon area.

They were followed by extensive *nuée ardente* eruptions emplacing the 'fragmental' toscanite series. This marked the formation of the ring fracture, the obliteration of lakes within the ring and the beginning of subsidence into the underlying magma chamber. The rise of the main 'nevadite-dacite' series along the ring fracture

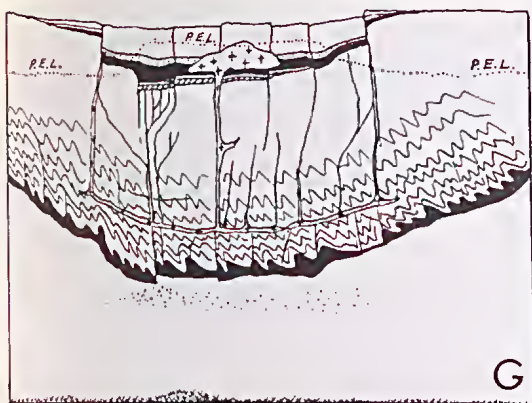


Fig. 10—Series of diagrams showing the development of the Cerberean Cauldron, based on an original model of Birch *et al.* (1970). The current model assumes the presence of a lower crustal silicic layer beneath Cambrian 'greenstones' (shown in black) and the folded Palaeozoic fill of the Melbourne Trough (see magma origin section for discussion of crustal structure). Partial melting is attributed to basic diapirism into this lower crustal layer. The diagrams are approximately to scale, except for the expanded thicknesses of the individual volcanic units. Fold styles and faults are diagrammatic only.

a, eruption of ash-flows forming the Snobs Creek Volcanics following partial melting of the lower crust. Some subsidence in the region, with movement along the Snobs Creek Fault. b, cessation of volcanism and the formation of lakes in the basin, with deposition of the Blue Range Formation. c, a renewal of volcanic activity with the widespread eruption of the andesites of the Torbreck Range Formation. These may have an upper mantle origin. A caldera, largely filled with andesites, developed on the Snobs Creek Fault. d, a return to acid ignimbritic volcanism with some associated andesitic lavas, forming the Robleys Spur Formation. Extensive partial melting in the lower crust, with accumulation of magma at higher levels. More marked regional subsidence commencing. e, continuous partial melting leading to a large differentiated magma chamber. Regional subsidence continuing. f, volatile saturation attained in upper levels of magma chamber leads to explosion generating radial and ring fractures. Crustal blocks subside into magma chamber accompanied by large scale ash-flow eruption of the Rubicon Rhyolite and Lake Mountain Rhyolite filling the 'cauldron'. g, upward migration of remaining magma to form ring and radial dykes and high level granodioritic intrusions into the base of the volcanic pile. Region stabilizes and erosion commences. (P.E.L. = Present erosion level)

then followed. Ultimately, the subsidence along the steeply outward-dipping ring fracture was 600-900 m, where measurable close to the fracture, but basining, evidenced by decreasing inward dips of the volcanic units up-sequence, indicated that a likely subsidence of 1600 m occurred at the centre of the block.

The mapping of the entire complex in the 1970s resulted in a number of modifications to this initial model, arising mainly from the discovery of a set of radial faults and the conclusion that all the acid volcanic units were ash-flows (Birch *et al.* 1970, 1978).

The essential points of the current model are outlined below and shown diagrammatically in Fig. 10.

1. The cauldron is a cylindrical block, which has subsided along an integrated pattern of circular and radial faults which essentially operated contemporaneously. Greater subsidence at the centre of the block has led to basining of the volcanic pile.

2. The earliest known fault associated with the cauldron structure is Snobs Creek Fault, which was operative during the emplacement of the first ash-flows (Snobs Creek Volcanics) (Fig. 10A). It was parallel to regional basement trends and was hinged, with opposite vertical displacements at either end.

3. An inner ring fracture, partially dyke filled and exposed on the northeastern margin of the cauldron, may represent an early-formed caldera centred on Snobs Creek Fault (Fig. 10C).

4. Source vents for the earliest ash-flows were probably associated with Snobs Creek Fault. The suspected early caldera may have been a vent for the basic-intermediate lavas of the Torbreck Range Formation. There is no direct evidence for the ring dyke being a source vent for the Robleys Spur Volcanics (incorporating the 'fragmental' toscanites) (Fig. 10C). Other feeders, either central vents or fissures, have probably been covered by the later ash-flows (Clarke *et al.* 1970). The Cerberean Volcanics were undoubtedly erupted from the outer ring fracture.

5. Basining and ring fracture components make up the overall subsidence. Early basining is indicated by decreasing inward dip of the volcanic units up sequence, as suggested by Thomas (1947), and the deposition of the lacustrine Blue Range Formation (Taggerty fish beds) (Fig. 10B). Thus, the region was probably under tension before failure took place along the ring fracture. Major subsidence along the ring fracture postdates the Rubicon Rhyolite, but subsidence probably occurred progressively throughout emplacement of the Cerberean Volcanics (Fig. 10F).

6. The evidence from the well-established steep outward dip of the ring-dyke is inconclusive for the establishment of a model for the origin of the fracture pattern. However, the overall ring and radial fracture pattern and the stretching of the foundered block suggest that the roof of the magma chamber behaved as a circular plate. A 'point' explosion at depth appears to best explain the fracture pattern, possibly as the magma attained volatile saturation in its upper region (Fig. 10F). Violent ash-flow eruptions then proceeded via the fractures and enabled wedge-shaped crustal fragments to subside, differentially, into the magma chamber as support was withdrawn.

7. High level magmas, in two main phases, intruded the base of the volcanic pile to the south (Fig. 10G). No resurgent volcanism is observed.

Modelling of the spacing geometry of volcanic and intrusive centres in the southern portion of the Lachlan fold belt by Rickard and Ward (1981) suggested the presence of an upper 'brittle' crustal layer averaging about 10 km thick. This layer modified the manner in which magmas derived from deeper levels in the crust were emplaced. Direct evidence for the existence of such

a layer may be seen in the foundered roof block of the Cerberean Cauldron, which behaved like a circular plate with a probable thickness less than half its diameter of 27 km. The above model is not entirely applicable to the other major subsidence structures in central Victoria, in that none show the regularity, cyclic volcanism or variable early sequences to the degree exhibited by the Cerberean, which is probably the most regular and best preserved Palaeozoic ash-flow/subsidence complex known. Taken as a group, however, the features shown by the central Victorian complexes are similar to those of Mesozoic and younger calc-alkaline complexes in the circum-Pacific belt, particularly in Chile, Nevada, Alaska, and New Zealand. Perhaps the most noticeable differences, neglecting any mineralogical or chemical distinctions, are the absence of extensive non- or poorly welded units, the scarcity of identifiable ash-fall beds, the unusually large thicknesses and the high phenocryst contents within the central Victorian sequences. The textural variations associated with base or pyroclastic surge (Wohletz & Sheridan 1979) are lacking in the major units, which are all densely welded and show relatively uniform vertical chemical and mineralogical variations (Birch 1978). Emplacement temperatures were therefore high, probably greater than 500°C (Clemens 1981), and there is no evidence for gravitational column collapse (Sparks & Wilson 1976) as a driving mechanism for the pyroclastic flows. Instead, the kinetic energy of the ash-flows was probably derived from the subsidence of the crustal blocks into the magma body. It is possible, however, that large volumes of ash-fall and non- or poorly-welded pyroclastic deposits originally blanketed much of the area between individual complexes, and have since been removed by erosion. Most of the complexes owe their preservation to downfaulting as much as to differential erosion rates.

OTHER VICTORIAN COMPLEXES

Comparison of the central Victorian complexes with major belts of acid volcanic rocks in western and eastern Victoria reveals major differences in age, structural control, mineralogical characteristics and degree of preservation. Most of the major belts outside the central region have not been investigated in detail and further work is desirable. From west to east, the main belts are as follows (See Fig. 1).

Rocklands (& Wickliffe) Rhyolite: This is a generally poorly exposed belt of rhyolitic rocks and pyroclastics, of unknown age, underlying the Siluro-Devonian sediments of the Grampians Group and overlying Cambro-Ordovician basement. The rhyolites average only about 2% phenocrysts (quartz and K feldspar) and are often characterised by a laminated appearance (Dennant 1893), with fine-scale continuous banding in alternating sodic and potassic layers (Hallenstein 1971). These are frequently highly contorted (Fig. 11). More massive porphyritic varieties outcrop in the Hamilton area (e.g. in Grange Burn). The rhyolites are essentially flat-lying but their mode of emplacement is uncertain,



Fig. 11 — Hand specimen showing contorted flow banding (?) in the Rocklands Rhyolite (NMV E4511). Specimen is 14 cm long.

although they may well be thick lava flows or coalescing domes (I. A. Nicholls pers. comm.). No collapse structures or vents are evident. Limited chemical data indicate an S-type character for the magmas.

Mt. Macedon Complex: The smallest of the Late Devonian central Victorian complexes, measuring about 8 by 8 km, it consists of a single rhyodacite unit at least 300 m thick which is mineralogically similar to the uppermost units in the Acheron Cauldron and Dandenongs Complex. A small granodiorite body has intruded the rhyodacite on the eastern side. Since no evidence for a ring fracture has been discovered, the rhyodacite probably represents the filling of a volcanic depression by ash-flow eruptions. No detailed investigation of textures within the rhyodacite has been undertaken since the descriptions by Gregory (1902) and Skeats and Summers (1912). However, a photomicrograph of a 'cryptocrystalline' 'hypersthene andesite' clearly shows eutaxitic textures (Skeats & Summers 1912, Fig. 2).

Strathbogie Complex (Violet Town Volcanics): The Violet Town Volcanics outcrops over 240 km² in northern Victoria, occupying an elliptical downwarp, and forming the northern component of the Late Devonian Strathbogie Complex (White 1954, Hills 1959). The simplified sequence within the volcanics consists of three ash-flow tuff units, beginning with a thin rhyolite (Fig. 12) grading to a rhyodacite. This is overlain by a thicker (100 m) rhyolite-rhyodacite unit and the uppermost unit is a uniform crystal-rich rhyodacite up to 200 m thick (Birch *et al.* 1977) almost identical to the Lake Mountain Rhyodacite in the Cerberean Cauldron. The rocks are extensively recrystallised, but sufficient primary textures are preserved to enable them to be identified as ash-flows (White 1963, Clemens 1981). The general structure of the Violet Town volcanics is sheet-like with a slight northward tilt but a marked upturn along the intrusive southern contact with the granite of the Strathbogie Batholith (Phillips *et al.* 1981).

Dandenong Ranges Complex: The volcanic rocks and

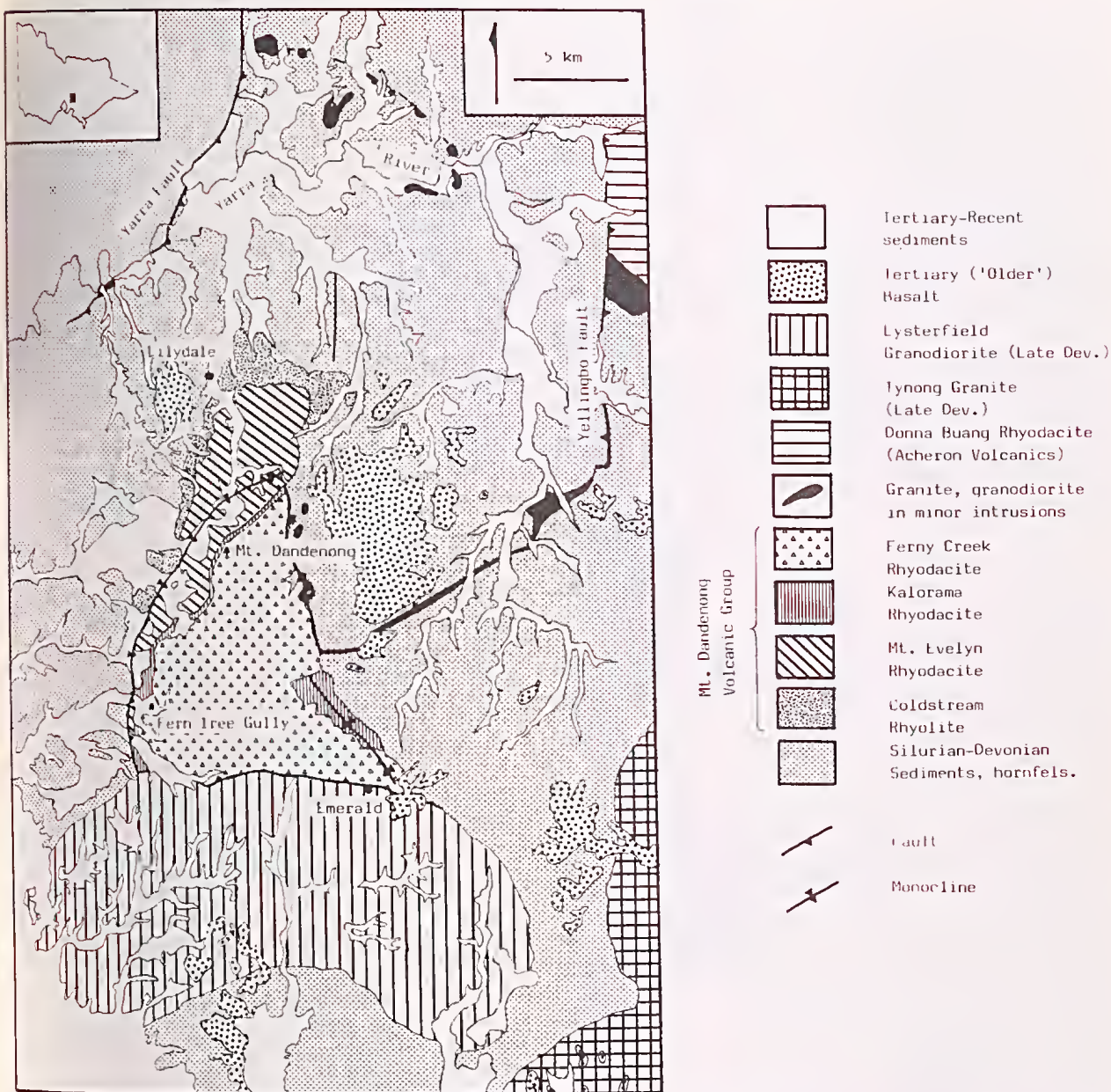


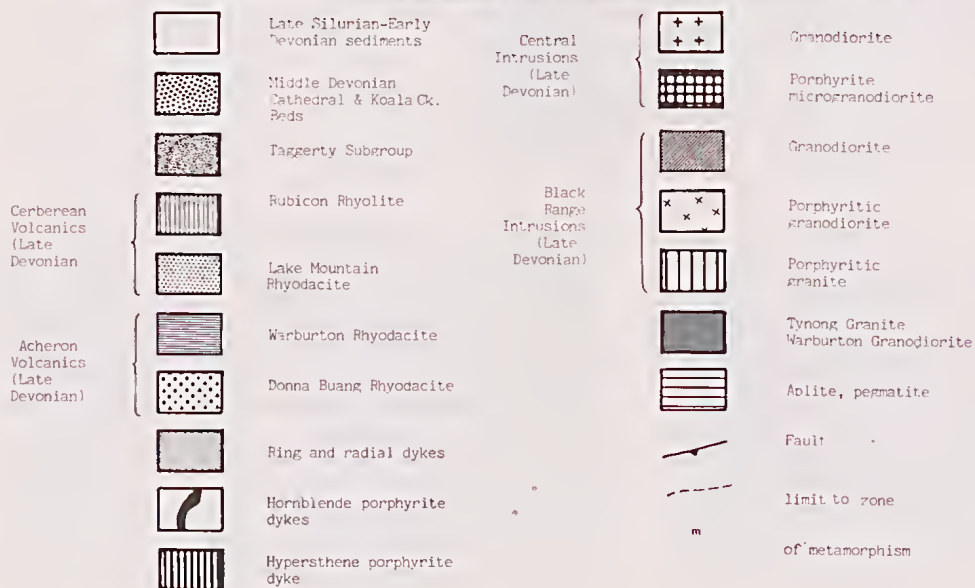
Fig. 13—Geological map of the Dandenongs Igneous Complex.

the granodiorite in this complex occupy a roughly triangular trough-like structure, 330 km² in area, which appears to be a simple syncline in the north, but is complicated by cross-cutting faults and monoclinical warps in the south (Fig. 13). Near vertical easterly dips occur in the volcanic rocks on the western margin (Hills, 1941), indicating severe post-emplacement subsidence. Early mineral analyses from the 'dacites' were undertaken by Richards (1909). The sequence was first subdivided by Morris (1914), described (as lavas) in detail by Edwards (1956) and revised by VandenBurg (1971). With the possible exception of the lowermost flow in the basal Coldstream 'Rhyolite' the volcanic rocks are thought to

be welded ash-flows (McLaughlin 1976). The Coldstream Rhyolite is overlain by a series of rhyolitic and rhyodacitic ash-flows forming the Mt Evelyn Rhyodacite. The main collapse phase is represented by two uniform rhyodacite units, the Ferny Creek Rhyodacite overlying the Kalorama Rhyodacite. There are some similarities between the general sequence in the Dandenongs Complex and the upper part of the sequence in the Acheron Cauldron, 16 km to the north. In particular, the Donna Buang Rhyodacite and Ferny Creek Rhyodacite appear equivalent. The southern margin of the volcanics is a fault contact with the Lysterfield granodiorite, along which the rhyodacites



Fig. 14—Geological map of the Marysville Igneous Complex (after Dudley *et al.* 1971, Birch *et al.* 1970).



have become schistose (Skeats, 1910). There is some evidence for an arcuate fracture, with a few pods of quartz porphyry, around the northern margin of the complex and possibly continuous with the main Yellingbo Fault cutting the volcanics (Fig. 13).

Marysville Igneous Complex (Cerberean and Acheron Cauldron): The Cerberean Cauldron (Fig. 14) has been discussed in sufficient detail above. The Acheron complex to the south was considered by Hills (1959) to be a hinged flap, with volcanics thickening to the south (Fig. 14). All the volcanic, chiefly rhyodacitic, units are welded ash-flows (Dudley *et al.* 1971) and a number of units are common to both (Table 1). The Acheron Cauldron subsidence probably occurred after the main Cerberean subsidence, as the youngest unit (the Donna Buang Rhyodacite) is absent from the latter. The style of subsidence is also different, with the foundered block of the Acheron delineated by generally straight fractures, juxtaposing volcanics with basement sediments, and suggesting some post-depositional subsidence.

The main intrusive phase includes a complex belt in the Black Range, to the northeast (Howard 1972), and an extensive granodiorite intruding the volcanic sequence in the junction region between the two cauldrons (Birch *et al.* 1978, Bini 1982) (Fig. 14).

Tolmie Highlands Complex: This Complex straddles the Mt. Wellington Axis, the eastern boundary of the Central Victorian Trough. Unlike other multi-unit complexes it consists almost entirely of rhyolitic rocks. Although Brown (1961) included the older Holland's Creek Rhyodacite (a welded ash-flow) and associated conglomerates and clastic sediments within the complex, these occupy an older depositional basin and are separated by a period of erosion and block faulting from the younger volcanic episodes (Clemens 1981, Gaul 1982). As mapped by Brown (1961), the volcanics occupy a basin, fault-bounded on its northeast, east and south margins, with a major northwest-southeast fault separating two sub-basins. More recent mapping (Gaul 1982) has suggested subsidence on a more rectilinear horst and graben-like basis, some of it post-depositional (Fig. 15). Rhyolitic rocks occur as two main thick ash-flow units, the Ryans Creek Rhyolite (Birch 1975, 1978) (Fig. 16) and the Toombullup 'Rhyodacite' (which is rhyolitic, at least in the lower portions). To the south, the contact between the two is sharp and may be marked by an ash-fall layer (Clemens 1981). In the north and northeast, the Ryans Creek Rhyolite fingers out, forming flat-lying hill cappings, and may show gradational contacts with the overlying Toombullup 'Rhyodacite'. A separate wedge-shaped rhyolitic unit (the Molyullah Rhyolite) overlies the Toombullup 'Rhyodacite' in a fault-bounded basin in the north (Gaul 1982, Birch *et al.* 1977). Isolated pods of intrusive rocks occur near the margins of the complex, but there is no semi-continuous ring dyke and no evidence for a ring fracture (Gaul 1982). A number of post-volcanic faults complicate the stratigraphy. The Barjarg Granite, the equivalent of the Strathbogie Batholith (Phillips *et al.* 1981), intrudes the volcanics in the southwest.

Wellington Rhyolites: A widespread, relatively uniform series of rhyolitic rocks occurs conformably within the Late Devonian-Early Carboniferous 'red-bed' sequences (Avon River Group) in the Macalister and Avon Synclinoria in east central Victoria (Neilson 1964). The rhyolites represent a single period of eruption and form a sheet-like unit up to 600 m thick. The outcrop area measures about 100 × 45 km, encompassing the two main basins. Weakly alkaline basalt flow sequences up to 400 m thick are interbedded with the sedimentary rocks both above and below the Wellington Rhyolite (Sutton 1978), which also contains a few thin basalt flows (Neilson 1976). No source vents for either rhyolite or basalt have been described.

Although a wide variety of textural terms have been used (e.g. Neilson 1976) the main variant is a pale, phenocryst-poor aphanitic rhyolite showing 'flow textures'. Early petrographic descriptions of 'fluidal' and pyroclastic textures by Skeats (1909) and Thiele (1908) are suggestive of eutaxitic textures. More recent studies (Sutton 1978, Buckley 1982) indicate that the rhyolites are variably welded and were emplaced by large scale ash-flows (Figs 17-19).

Jemba Rhyolite: Hills (1959) recognised the Jemba Rhyolite as a cauldron subsidence region and it is the only occurrence in eastern Victoria where there is clear evidence for both cauldron subsidence and ash-flow emplacement (Fig. 20). It is also the oldest complex of this type in Victoria, being dated at 400 Ma (Richards & Singleton 1981; corrected data of Brooks & Leggo 1972).

The Jemba Rhyolite forms a prominent plateau of 65 km² and elliptical in outline. It consists entirely of rhyolitic rocks, the sequence being up to 650 m thick. A welded crystal-rich rhyolitic ash flow forms a single cooling unit over 400 m thick. Although primary eutaxitic and vitroclastic textures are preserved at the base of this unit—Leggo (1968) first described recrystallised 'ignimbrites' from the basal zones—these are rapidly obliterated by recrystallisation upwards in the unit (Birch 1975, 1978; Figs 21 & 22). Thin rhyolitic ash-fall and rhyolite flow units outcrop at the base of the sequence in the north (Oates & Price 1983). Chemical and mineralogical trends within the main mass have been discussed by Birch (1978), Oates (1980), and Oates and Price (1983). An arcuate ring fracture within the Late Ordovician metasedimentary basement completely encloses the rhyolite and is marked by about ten small granitic intrusions (Fig. 20).

Mitta Mitta Volcanics: The volcanic rocks in the Mitta Mitta graben, north of Benambra, occur in three separate belts (I. A. Nicholls pers. comm.), apparently separated by faults and extending for about 45 km. In the southernmost belt, phenocryst-poor acid volcanics outcrop as steep cliffs in the valley of the Mitta Mitta River (Bolger 1982). Recrystallisation is extensive and there is little evidence for emplacement mechanisms. The volcanics may be lavas (Cook 1978). In the central belt (Larsen Creek and the Dart River), a wide range of mass-flow breccias, ash-flow tuffs, minor lavas and in-

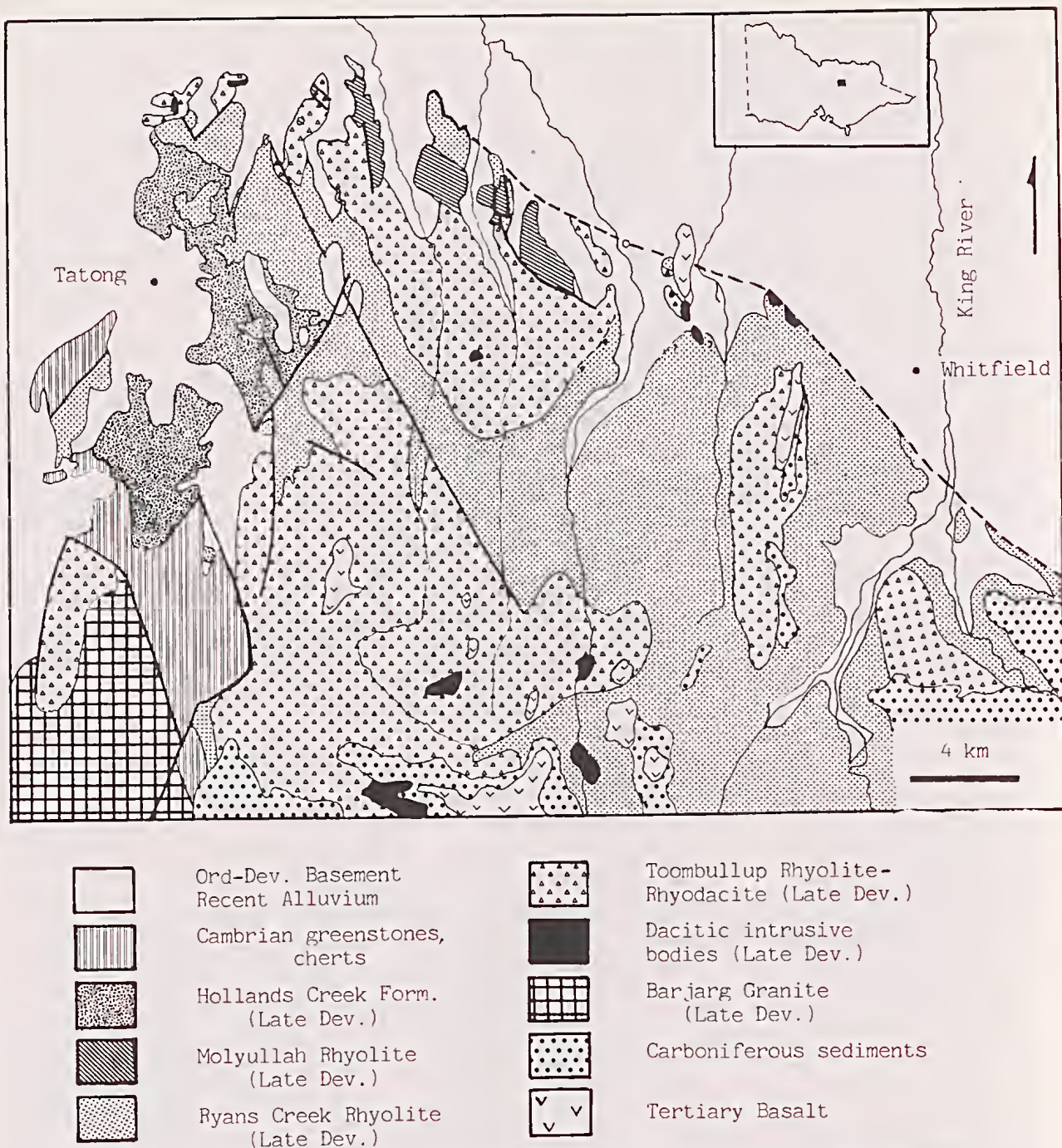


Fig. 15—Geological map of the northern portion of the Tolmie Highlands Complex (after Gaul 1982, Brown 1961).

trusive rocks are exposed. Well-developed eutaxitic textures are preserved in dacitic-rhyodacitic ash-flows (Bolger 1979, I. A. Nicholls pers. comm.). In the northern belt, near Mt. Benambra, a thick sequence of crystal-rich rhyolitic ash-flow tuffs occurs. The rocks within the southern belt of the Mitta Mitta Volcanics are similar to those in the Thorkidaan Volcanics, and both are probably Middle-Late Silurian (VandenBerg *et al.*

1979). The central and northern belts may be Early Devonian (P. Bolger pers. comm., I. A. Nicholls pers. comm.).

Thorkidaan Volcanics: These form a broad, northeast-southwest trending belt, 30 × 10 km, in the Limestone Creek area in northeastern Victoria. They consist of a thick sequence of rhyolites with minor rhyodacite, and

ash-fall and possibly fluviatile tuffs. The volcanics are variable in appearance and phenocryst size and abundance. Despite the extensive recrystallisation, chloritisation and sericitisation affecting the groundmass, sufficient textural evidence is preserved to indicate an ash-flow origin for many of the rocks (VandenBerg *et al.* 1979) (Fig. 23). However, autobrecciated and flow-banded rhyolitic lavas are also present, particularly in the Tambo Valley, near Bindi (Lew 1979). The Thorakidaan Volcanics are tentatively placed in the Middle to Late Silurian. The Silurian sequence of which they are a part is unconformably overlain by the main north-south belt of Snowy River Volcanics.

Snowy River Volcanics: This is the most voluminous series of acid volcanic rocks in the state, with the main outcrop being an irregular north-south trending belt, 110 km long and up to 50 km wide, extending from Limestone Creek and Suggan Buggan to Nowa Nowa, in eastern Victoria. They are stratigraphically dated as Early Devonian and the major rock types are porphyritic rhyodacite and dacite, with minor rhyolites, andesites, basalts and intercalated sediments (Ringwood 1955, Tattam 1976). The rhyolites and rhyodacites frequently show eutaxitic textures and much of the formation represents extensive ash-flow sheets preserved, not by cauldron subsidence, but by contemporaneous and subsequent rectilinear faulting (Talent 1965). A wide range of debris flows, lahars, lag breccias and lacustrine sediments is also present (Orth 1982). Despite widespread alteration, including albitisation, silicification and chloritisation, textures in the Snowy River Volcanics are much better preserved than in the Thorakidaan Volcanics.

Other Occurrences: Minor occurrences of mainly Late Devonian acid volcanics interbedded within sedimentary sequences are known outside the main belts. For example, rhyolite and rhyodacite ash-flow units occur at Mt. Timbertop, Mt. Cobbler, The Bluff-Bindaree and in the South Blue Range in the northern region of the Mt. Howitt Province. Garnet-bearing rhyodacite units have been mapped in the Bendock area, further east (P. Bolger pers. comm.). Occasional pebbles of acid volcanic rocks, sometimes with eutaxitic textures (Fig. 24) occur in the Permian glacial deposits in central Victoria. A small inlier of hornblende and biotite-bearing dacite and rhyodacite occurs within granodiorite at Dromana on the Mornington Peninsula (Baker 1938).

PETROGENETIC IMPLICATIONS

Continuous generation of acid magmas, and their emplacement by ash-flow, ash-fall and lava-flow (as well as intrusive) mechanisms occurred in the Victorian region from the Middle-Late Silurian to the Late Devonian. There are, however, significant differences between the so-called central Victorian complexes (Macedon, Marysville, Strathbogie, Tolmie and Dandenongs) and the western and eastern belts (Rocklands, Wellington, Jemba, Mitta Mitta, Thorakidaan, Snowy River), particularly with respect to age, periodicity, structural style and mineralogy.

AGE: The central Victorian complexes are Late Devonian, while the western and eastern belts span at least the period Late Silurian to Early Devonian.

PERIODICITY: There is an apparent absence of cyclic activity in the western and eastern occurrences, although not all the central complexes show periodicity to the same degree.

STRUCTURAL STYLE: The central Victorian complexes are associated with roughly equidimensional collapse structures, bounded either by a clearly marked ring fracture, by one or more fault systems which may have been differentially active, or by monoclinical warping. Only the Jemba Rhyolite of the eastern occurrences is clearly bounded by a ring fracture. The remainder appear to occupy roughly linear graben-like structures.

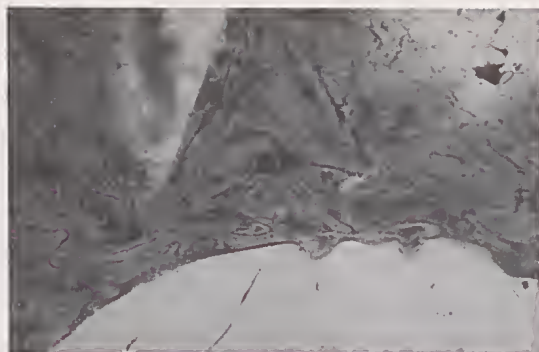
MINERALOGY: The rock types in the central complexes are characterised by iron-rich assemblages including biotite, garnet, cordierite, orthopyroxene and, less commonly, fayalite. The eastern and western sequences, are generally less iron-rich and aluminous and tend to be monotonous in their phenocryst mineralogy which often involves quartz, two feldspars and small, varying amounts of biotite. However, dacitic ash-flows within the Snowy River and Mitta Mitta volcanics may contain phenocrysts of hypersthene, augite and hornblende (I. A. Nicholls, pers. comm.).

CHEMISTRY AND MINERALOGY

The general chemical characteristics of the central Victorian volcanic rocks are now well established. They can be summarised as: high silica contents (most analyses show more than 65% SiO₂), high aluminium and low calcium contents (reflected in normative corundum and hypersthene), high Fe/Mg and generally high K₂O/Na₂O ratios. The chemical (and mineralogical) features show clear affinities with S-type granitic liquids (Chappell & White 1974); i.e. all rhyolitic rocks (with >72% SiO₂) from the major central Victorian complexes have Na₂O < 3.2% for K₂O ≥ 5%, Mol. Al₂O₃/(CaO + Na₂O + K₂O) > 1.1 and CIPW normative corundum > 1%. I-type magmas (Chappell & White 1974) appear to be absent from the central Victorian belt.

Chemical variation is most marked in the rhyolitic rock types (72 to 78% SiO₂), which show increasing K₂O, CaO, Ba and Sr and decreasing Rb and Na with increasing sample height within a particular stratigraphic sequence (Birch 1975). The rhyodacitic units tend to be more uniform. The Donna Buang Rhyodacite and its probably equivalent, Ferny Creek Rhyodacite, are the most basic (av. 64% SiO₂) and limited data (Skeats & Summers, 1912) suggest that the Macedon Rhyodacite is similar. The Lake Mountain Rhyodacite and the upper Rhyodacite unit in the Violet Town Volcanics are more acidic (av. 69% SiO₂). The misnamed Toombullup Rhyodacite is actually a rhyolite with 70-72% SiO₂.

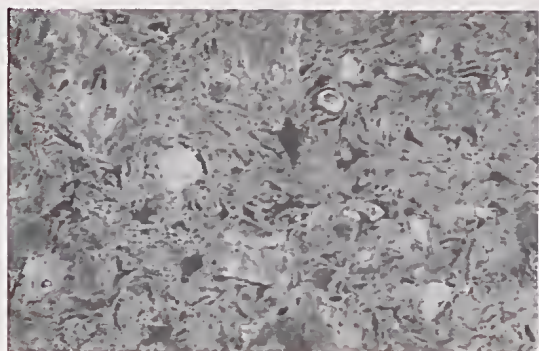
The chemistry of the western and eastern acid volcanic belts is not well known. Limited data indicate that the Rocklands Rhyolite is S-type (Hallenstein,



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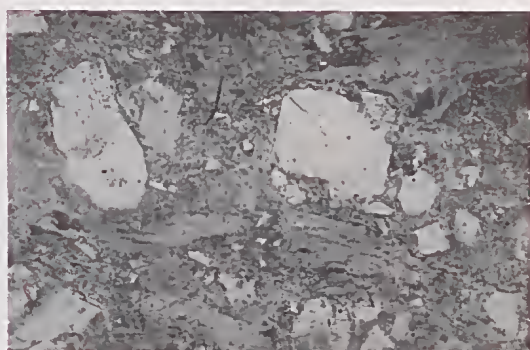
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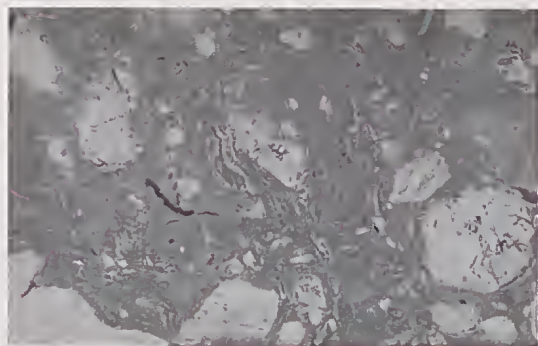
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1971). The Jemba Rhyolite is weakly peraluminous and cannot be classed as either S or I type (Oates & Price 1983). The only published chemical data on the other eastern belts are a few analyses of intermediate rocks of the Snowy River Volcanics near Buchan (Cochrane & Sampson 1950). However, unpublished petrographical and analytical studies on the Mitta Mitta Volcanics (central belt) and the Snowy River Volcanics (Porritt 1976, Sielecki 1980) indicate I-type mineralogical characteristics (hornblende and clinopyroxene phenocrysts in dacites and rhyodacites) with transitional geochemical features (weakly diopside normative to weakly corundum normative) (I. A. Nicholls, pers. comm.).

The rocks in the central Victorian complexes consist of various phenocrysts in a quartz-feldspathic groundmass of rhyolitic composition (Edwards 1956). Quartz is the dominant phase, along with K feldspar (Or₆₀ to Or₇₅ in the rhyolitic rocks) and zoned plagioclase (An₃₅-An₅₅ in the rhyodacites, An₁₀-An₆₀ in the rhyolites) (Birch *et al.* 1977).

The ferromagnesian assemblages are typically S-type, dominated by biotite-orthopyroxene \pm garnet in the rhyodacites and biotite \pm garnet \pm cordierite in the rhyolites (Birch *et al.* 1977). Iron-rich garnets are widespread and may be grouped on the basis of their zonation and composition (Birch & Gleadow 1974, Birch 1975, Clemens 1981). Iron-rich cordierite is present in the Rubicon, Ryans Creek and basal Strathbogie Rhyolites, while a more magnesian cordierite occurs in some of the rhyodacites (Dudley 1971). Biotite is more iron-rich in the rhyolitic rocks and orthopyroxene is generally hypersthene. The Toombullup 'Rhyodacite' contains the most diverse ferromagnesian assemblages, with biotite, several garnet types, two varieties of hypersthene (R. Dudley pers. comm.) and fayalite (Brown 1961, Clemens 1981). The western and eastern acid volcanic belts (including the Jemba Rhyolite) apparently do not contain these diverse ferromagnesian assemblages. More acid rocks in these belts normally carry biotite as the only mafic phenocryst.

MAGMA ORIGIN

In his discussions of the various acid volcanic complexes, Hills concentrated on their structural development rather than the origins of the magma. In his 1959 paper, he appealed to a single parent magma of acid-intermediate composition for all the complexes, but suggested that it was generated elsewhere and injected beneath the region. Hills regarded the late Middle Devo-

nian Woods Point Dyke Swarm, chiefly of diorites and lamprophyres (Hills 1952) as 'fore-runners of an advancing wedge of magma moving from the east to the northwest'. He considered that differentiation in this magma body had produced the vertical gradation from rhyolite to 'dacite' and that the parent magma was very fluid (presumably to enable it to erupt as 'lavas'), free of xenoliths and was crystallising intratellurically when it erupted. Edwards (1937, 1956) had discussed the likely origin of the parent magma for the quartz diorites, granitic intrusions and lavas of eastern Victoria in terms of assimilation of argillaceous crustal rocks by basaltic (tholeiitic) magma, followed by crystallisation differentiation. White (1954) proposed widespread assimilation of alumina-rich sediments and thorough mixing of large amounts of contaminated basaltic magma rising slowly through the crust. The idea of dacitic magma injected beneath the region was still current in the mid 1960s, judging by the conclusions reached by Valiullah (1964) in his study of the rhyolite-dacite suite.

Over the last 10 years, the more intensive investigation of the chemistry and mineralogy of the central Victorian volcanic-intrusive complexes has resulted in a general consensus view that the parent magmas were anatectic in origin (Phillips *et al.* 1981). A number of lines of evidence, some already referred to, indicate that the parent rocks were broadly pelitic to quartz-feldspathic metasediments. The general conformity of the major and trace element parameters with so-called 'crustal' values, the peraluminous nature of the rocks (most are corundum/hypersthene normative), their overall 'S-type' character, and initial Sr⁸⁷/Sr⁸⁶ ratios of at least 0.710, (Brooks & Leggo 1972, McDougall *et al.* 1966), all suggested derivation of magmas from an evolved crustal source region.

Conditions under which the partial melting took place have been investigated using evidence from experimental work on natural granite compositions (e.g. Clemens & Wall 1979, 1981) and partition relations within the ferromagnesian suite (e.g. Clemens 1981, Birch & Gleadow 1974). Subtle differences in chemistry and mineralogy between individual complexes in central Victoria reflect variation in the nature of the source rocks and the conditions of melting. Nevertheless, the data suggest pressures and temperatures at least as high as 4-6 kbar and of 800-900°C and water-undersaturated conditions for magma genesis (e.g. Phillips *et al.* 1981, Clemens & Wall 1979). These are equivalent to depths of 17-25 km, indicating very high geothermal gradients.

Figs 12, 16-19, 21-23—12, vitroclastic textures within the basal rhyolite of the Violet Town Volcanics. 16, well preserved flattened shards in the Ryans Creek Rhyolite, 5 km east of Tatong. 17, vitroclastic textures in a specimen of the Wellington Rhyolite (NMV E10807), from Shanty Hollow, near Mt. Ken. The shards are replaced by a chloritic alteration product. 18, part of a flattened pumice fragment in the Wellington Rhyolite (NMV E10830). 19, specimen of Wellington Rhyolite (E10804), altered but showing occasional cusp-shaped fragments, indicative of original glass shards. 21, eutaxitic texture in the basal zone of the Jemba Rhyolite. The small pumice fragments are moderately flattened. 22, well preserved, contorted, flattened devitrified glass shards in the basal zone of the Jemba Rhyolite. 23, dense welding textures in the groundmass of a specimen of the Thorkidaan Volcanics (NMV E10706).

Note: Field of view is 0.9×0.6 mm in Figs. 12 & 16. Field of view is 3.5×2.3 mm in Figs. 17-19, 21-23.

There are few published interpretations of the origin of magmas for the acid volcanic belts in eastern or western Victoria. However, the distinctive major and trace element chemistry of the Jemba Rhyolite was attributed by Oates and Price (1983) to partial melting of refractory crustal material, from which granitic melts had previously been removed.

There are three possible origins for the fundamental structural chemical variation shown by the Victorian acid magmas. These involve either a progressive separation of refractory phases from a granitic liquid of 'minimum melt' composition, a fractionation model involving products of magmatic crystallisation (including a degree of volatile transfer) or progressive partial melting in which removal of melt fractions becoming less silicic and more mafic took place. Given the size of the source region and the volume of magma produced, all three processes probably contributed to varying degrees.

The trigger for partial melting is uncertain in most cases, although it may well have been initiated by the diapiric upwelling, at various intervals throughout the early to middle Palaeozoic, of mantle-derived basic magma into the lower crust (Clemens & Wall 1981, Phillips *et al.* 1981). Basic rocks, admittedly in volumetrically minor amounts, are associated with many of the acid volcanic belts in the east. For example, basaltic rocks occur within the Snowy River Volcanics and the Wellington Rhyolites. An unfaulted belt of mainly andesitic rocks of uncertain age (the Bumble Creek Andesites) is associated with the Thorkidaan Volcanics (VandenBerg *et al.* 1981). A dyke swarm, ranging from dioritic to doleritic, preceded the emplacement of the Jemba Rhyolite (Brooks & Leggo 1972). In central Victoria, the Woods Point Dyke Swarm, with rock types ranging from intermediate to ultrabasic (Hills 1952), was emplaced immediately prior to the main acid volcanic episodes, while basaltic andesites are represented within the Cerberean Cauldron sequence.

The generation of acid-intermediate magmas across Victoria throughout the early to middle Palaeozoic must be considered in relation to the complex crustal processes affecting the region during that time. For the Silurian to Lower Devonian magmas in eastern Victoria, Richards and Singleton (1981) suggested that partial melting took place below an island arc. This influenced the tectonic pattern, chiefly by protecting the sedimentary fill between it and the shield to the west, from the Late Ordovician until the Early Devonian. Acid magmas were then generated in both the west, where they are of mixed S and I-type, and in the east, where they are dominantly I-type (I. A. Nicholls pers. comm. 1982), even though these fall to the west (i.e., S-side) of the S-I line projected from New South Wales (Chappell & White 1976).

Crawford (1983 and in prep.) significantly extended the model, in both time and space, in an attempt to resolve the apparently contradictory situation in which oceanic lithosphere, now represented by the Victorian Cambrian 'greenstone' belts (Fig. 1), is associated with

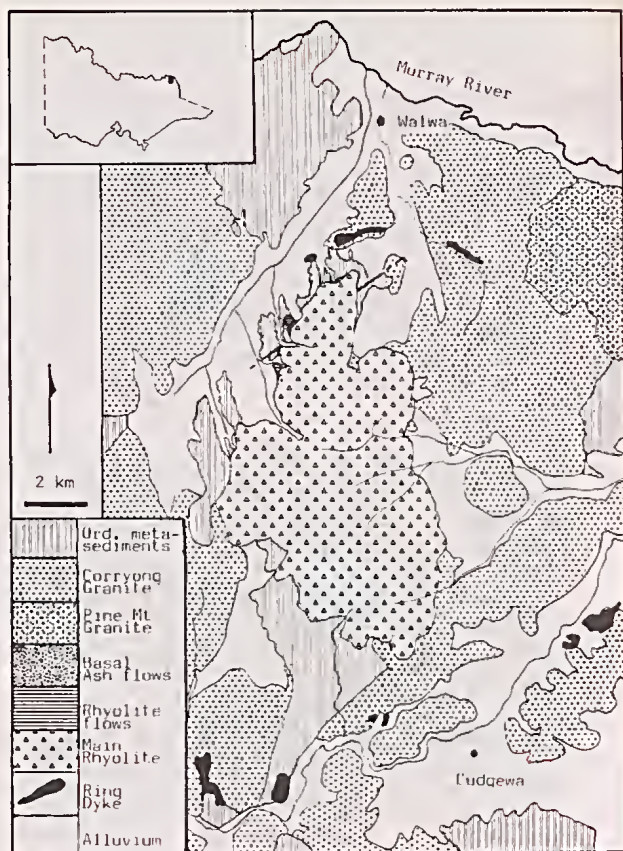


Fig. 20—Geological map of the Jemba Rhyolite (after Leggo 1964, Oates & Price 1983).

crustal thicknesses of a 'continental' scale (35–50 km) across Victoria (Cleary 1973, Gibson *et al.* 1981, Rickard & Ward 1981, Finlayson *et al.* 1980, Finlayson & McCracken 1981). The Crawford model invokes a series of island arcs and backarc basins developing eastwards across Victoria from the late Precambrian to the early Palaeozoic. The culmination of progressive westward subduction during this period was the underthrusting from east to west of thinned continental margin sialic crust, leading to overall crustal thickening and the generation of acid and intermediate magmas. This model would allow for the fact that estimates of the thickness of the Palaeozoic sedimentary cover (Cambrian–Late Devonian) across Victoria are neither sufficiently large (less than 15 km) nor reliable to support a magma origin by partial melting of the base of the sequence. Instead, an attenuated wedge of high grade Precambrian metasediments, beneath the Cambrian greenstones, and more or less continuous across Victoria, is the more likely source region (Clemens & Wall 1979, Phillips *et al.* 1981). Such a crustal thickening process, with its associated increased thermal gradients, could provide an alternative mechanism for anatexis. A logical extension of such a model would be to relate, in more detail, the various stages of crustal reorganisation to dated episodes of acid-intermediate magma genesis

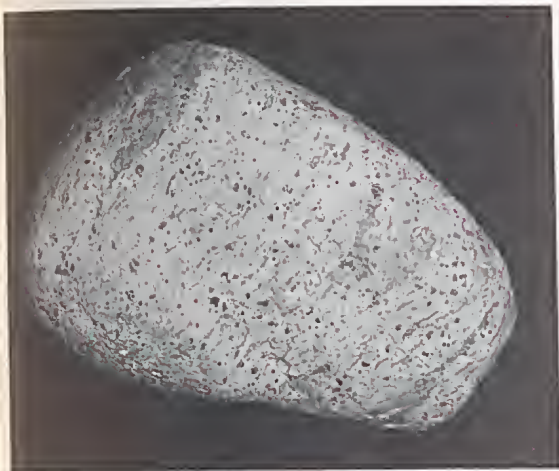


Fig. 24—Pebble of rhyolite showing eutaxitic textures, from the Permian glacial till at Derrinal, Victoria. Specimen is 16 cm long (NMV E10733).

across Victoria. This would include the central Victorian complexes, which at present appear to be inexplicable in terms of an island arc-subduction zone model.

CONCLUSIONS

Since the pioneering efforts of E. W. Skeats and E. S. Hills, the Palaeozoic acid volcanic complexes have been recognised as one of the major features of Victorian geology. Whereas, in the period up until 1960, their significance was discussed in terms of structural features and stratigraphy, the last twenty years have seen their chemistry and mineralogy generate considerable interest. There is little doubt that the Victorian acid volcanic rocks, and in particular their ferromagnesian assemblages, provide a key to understanding some of the processes by which metasedimentary sequences become acid magmas. Hills' devotion to a wide variety of geological themes has seen him have little direct involvement in the second stage of the overall study. Nevertheless, the petrographical, mineralogical and geochemical features of the acid volcanics cannot be studied in isolation, without reference to a stratigraphic sequence or a structural model. Hills' role in establishing the most significant sequences, developing the cauldron subsidence model and encouraging studies in other complexes was fundamental to the present state of knowledge.

The principles of ash-flow volcanism and the criteria by which it is recognised have still not gained universal acceptance within Victoria. This need not be due to entrenched attitudes, but to a failure of those aware of the contemporary developments to communicate them adequately. The problem is best illustrated by misuse of terminology, such as when a sequence is said to consist of 'rhyolite, tuffs and ignimbrites'. This is not the least of the challenges confronting those working locally in the field of acid magma genesis.

ACKNOWLEDGEMENTS

I am grateful for the critical comments of Drs. A. J. W. Gleadow, T. A. Darragh and I. A. Nicholls in reading the original manuscript of this review. In addition, Dr Nicholls contributed unpublished information on the volcanic rocks in the eastern belts, particularly the Mitta Mitta Volcanics.

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SHORELINE CHANGES IN THE GIPPSLAND LAKES 1957-1983

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ABSTRACT: In 1982-83 the shoreline of the Gippsland Lakes was re-surveyed at locations originally mapped in 1957-59 to determine the extent of advance or retreat over the intervening period. It was found that shoreline erosion had become more extensive, with many sectors of sandy, swampy or deltaic shoreline having retreated at least 2 m: on the Mitchell delta recession has been up to 5 m, and on the Tambo delta up to 30 m in the past 25 years. Progradation has been confined to a few sectors where swamp encroachment continues, and where sand has accumulated on spits and in embayments. Several sectors, including the shoreline of the Mitchell delta, have been stabilised artificially. It is predicted that the Gippsland Lakes shoreline will become increasingly sandy as sand loads moving down the Latrobe, Avon and Tambo Rivers begin to flow into the Lakes. Dumping of dredged sand on the lake shores is also increasing the extent of sandy beaches, but could have adverse ecological and environmental effects.

It is now well established that the coastal lagoons known as the Gippsland Lakes (Fig. 1) in eastern Victoria developed as the result of the successive deposition of sandy barrier formations across a broad marine embayment on the East Gippsland coast in Late Quaternary times (Bird 1965, 1978, Jenkin 1968). Enclosure of the existing lagoons (Lakes Wellington, Victoria, King and Reeve) occurred in Holocene times when, as a sequel to the major marine transgression that produced the broad outlines of the present coast, an outer sandy barrier formed, with the Ninety Mile Beach on its seaward side. When European explorers reached this area in the eighteen-forties the Gippsland Lakes had only a variable and intermittent outlet to the sea east of the township of Lakes Entrance, but in 1889 a permanent artificial entrance was opened (Bird & Lennon 1973), and the lakes, until then relatively fresh water systems, became estuarine lagoons.

Previous studies have shown that the Gippsland Lakes, enclosed behind and between sandy barrier formations, have shorelines which are being shaped by several processes: 1, wave action, which has cut out embayments and built up beaches and spits. In some areas the cutting of bays and growth of intervening spits has proceeded in such a way as to convert the previously long, narrow lagoons into chains of smaller, more rounded lagoons, a process termed segmentation (Zenkovich 1967); 2, current action, which has contributed to this segmenting process, and also initiated meandering of narrow straits, especially in the more tidal eastern region, where Hopetoun Channel winds towards Lakes Entrance; 3, swamp encroachment, initiated by the growth of reedswamp (mainly *Phragmites*, accompanied by *Typha*, *Cladium*, and other plants) in shallow nearshore water, prograding depositional terraces that are invaded by swamp scrub (mainly *Melaleuca ericifolia*); 4, fluvial sedimentation, notably at the mouths of the Mitchell, Tambo, Avon and Latrobe Rivers; and 5, deposition of sandy material washed or blown over narrow sections of the outer barrier, particularly in Bunga Arm and Cunningham Arm.

As a sequel to increased salinity in the Gippsland Lakes since the opening of the artificial entrance, much of the reedswamp fringe has died back, and erosion has ensued on low-lying swampy and deltaic shorelines around Lake King and Lake Victoria, and to a lesser extent in the relatively fresh Lake Wellington. This sequence was described and discussed by Bird (1978) on the basis of detailed field studies in 1957-59 and subsequent investigations.

In the summer of 1982-83 the shorelines of the Gippsland Lakes were revisited to assess the nature and extent of changes since 1957-59, especially on sectors that were surveyed and photographed during the earlier field studies. Attempts to measure shoreline changes from air photographs of various dates and scales were not successful because it is rarely possible to determine changes within ± 2 m by this method. Measurements were therefore made with reference to identifiable fixed points on the 1957-59 surveys which could still be located on the ground. It is difficult to make precise measurements of changes on cliffed shorelines of intricate outline (minor bays, promontories, and stacks), or on sandy beaches where the waterline can vary by up to 3 m horizontally in relation to oscillations of the lake level. Given these constraints it was decided to classify the shoreline into three categories: stable, advance or retreat of less than 2 m, and advance or retreat of more than 2 m over the past 25 years (Fig. 1). The present paper summarises the evidence for these changes, and discusses further changes likely to take place in the next few decades.

SHORELINE CHANGES

LAKE WELLINGTON

Erosion has become more extensive on the shoreline of Lake Wellington since 1957, largely because of further reductions in the extent and vigour of reedswamp growth, and the onset of wave scour on swampy terrain no longer protected by a reedswamp fringe. This is particularly evident on the southern shore of the lake, which now has only a few scattered stands of reedswamp, and on the western side of the Avon delta,



Fig. 2—The beach on the eastern shore of Lake Wellington has prograded by about 3 m in the period between May 1958 and May 1983, when this picture was taken. Repeated transects along the fence line have shown an advance of the shoreline and the development of a wide backshore zone of marram grass here during this period.

Photo: Eric C. F. Bird.

which has lost much of the reed fringe that existed in 1957. In both cases swamp scrub land, no longer protected by a reedswamp fringe, is being eroded by wave action. Where the reedswamp fringe persists, as on the eastern side of the Avon delta and around the mouth of the Latrobe River, accretion of silt and clay within this fringing vegetation has continued to advance the shoreline: at the mouth of the Latrobe, sedimentation in reedswamp has led to an advance of about 20 m since 1957.

The reduction in extent of reedswamp on the shores of Lake Wellington is probably related to variations in water salinity in this lake during the past 25 years. Much of the salt in Lake Wellington is derived from the inflow of sea water through the artificial entrance, diluted as it spreads through Lakes King and Victoria and into Lake Wellington by way of McLennan Strait. There are also minor and local accessions of brackish water from creeks and drains that discharge runoff from bordering salt marshes and saline flats, notably the drain from Lake Kakydra into Lake Wellington west of Marlay Point. Nevertheless, Lake Wellington remains the least brackish of the Gippsland Lakes, being remote from the artificial entrance. In 1958 surface water salinity in the middle of this lake ranged from a maximum of 12.0‰ in June to a minimum of 0.1‰ in December, typical of a seasonal fluctuation related to diminished rainfall and runoff and increased evaporation in summer and autumn (maximum salinity May-June), followed by increased freshwater inputs in winter and spring (minimum salinity November-December). Occasionally, as in February 1971, heavy rainfall in the catchments of the Latrobe and Avon Rivers results in the discharge of floodwaters into Lake Wellington, which is thus temporarily freshened. During droughts, on the other hand,

surface water salinity increases in Lake Wellington: during the 1967-68 and 1982-83 droughts it rose to more than 20‰ in the middle of the lake.

The possibility of an overall increase in the salinity of Lake Wellington in recent decades was suggested by Bird (1978) on the grounds that mean monthly surface salinity in 1957-60 was generally below the 20-year (1957-76) average whereas equivalent means in 1972-76 were above it. However, a more detailed statistical analysis by Mobley *et al.* (1983) failed to substantiate such an increase, and it now seems likely that impeded growth and die-back of reedswamp on the shores of Lake Wellington is due to the recurrence of high salinity in dry years (Clucas 1980). During the dry summer of 1982-83, when die-back of reedswamp was observed at several locations on the shores of Lake Wellington, salinity measurements in the southeastern part of the lake, off Plover Point, rose to a maximum of 22.5‰ in April 1983.

Surveys made in 1982-83, on transects originally mapped in 1957-59, indicate that much of the swampy shoreline around Lake Wellington has receded by up to 2 m, while near Marlay Point, and west of Plover Point, swampy shorelines have retreated by up to 3.5 m. In recent years, walls have been built to halt the shoreline recession at Marlay Point.

Sectors of the Lake Wellington shoreline bordered by sandy beaches have changed only slightly during the past 25 years. Sand eroded from the cliffs at Roseneath Point has been carried southwards to prograde the beach on the eastern shoreline by up to 3 m (Fig. 2) and sand accretion on Plover Point has built up a cusped foreland. On parts of the southern shoreline, sand has been washed up on to bordering swamp land to form chenier-like ridges behind low receding cliffs cut in

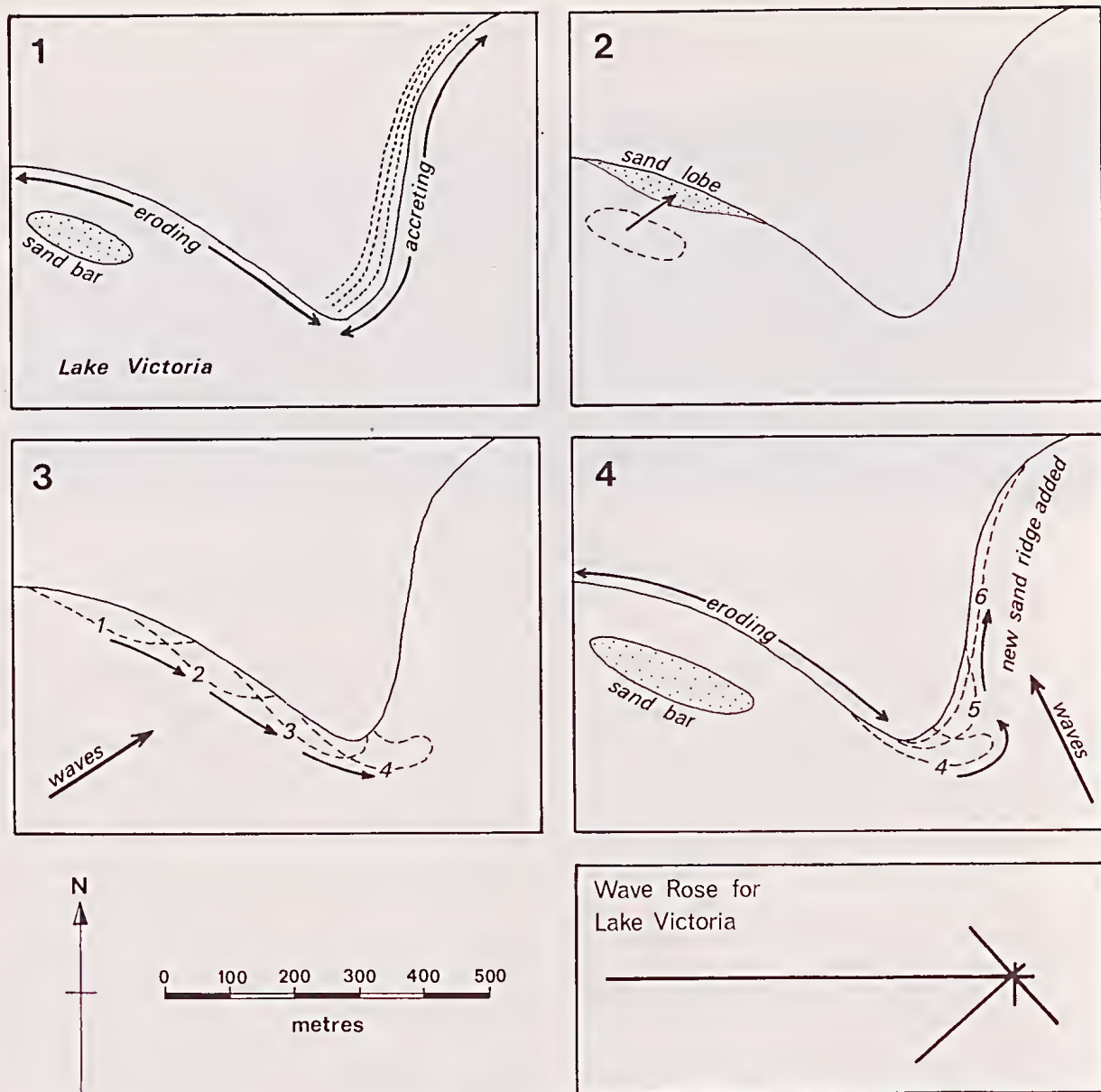


Fig. 3 — Sequence on changes on cusped forelands on the north shore of Lake Victoria, notably at Waddy Point (after Woodburn 1978).

swamp deposits. On Tucker Point the fine gray sandy beach has evidently been derived from sandy sediment of similar colour washed into Lake Wellington by the Latrobe River during floods. Studies of sandy sediment moving down the Latrobe indicate that this supply will increase in the future. Successive floods have already moved large quantities of sand down the river channel to below Rosedale, and the date of arrival of this material at the river mouth will depend on the frequency and severity of future flooding (Bird *et al.* 1979). The same is true of the Avon, which in the 1971 floods delivered a large shoal of sand to the lake floor south of Strathfieldsaye. This was subsequently re-worked by

wave action and carried on to lake-shore beach sectors at Marlay Point and Swell Point (Bird 1972). Such sand, travelling as bed-load, is not retained in the reed fringe at the mouth of the river; it is the suspended material, silt and clay, which becomes trapped in bordering reedswamp and thus added to the delta shoreline. In due course the augmented sand loads from the Latrobe and the Avon will nourish more extensive sandy beaches on sectors of the Lake Wellington shoreline that are at present swampy. It is also possible that the arrival of large quantities of sand at the mouths of these rivers will result in the growth of new, sandy deltas, the evolution of which will not depend on the presence of a reedswamp fringe.

LAKE VICTORIA

Much of the swampy shoreline of Lake Victoria was already eroding in 1957. Erosion has continued, especially in the western part of the lake, north of the delta at the eastern end of McLennan Strait, where the reedswamp fringe present in 1957 has disappeared, and shoreline recession of up to 3 m has ensued. Cluffed sectors of the sandy shoreline of the inner barrier, which forms the southern boundary of this lake, have also retreated by up to 3 m, although the recession of several cliffs cut into dune sand has been reduced by the introduction of shore protection works, mainly timber fencing and brushwood groynes.

The most obvious changes have occurred on spits and cusped forelands, mainly along the northern shore of this lake, which shows a succession of these depositional features between eroded bays. Woodburn (1978) examined the evolution and dynamics of Storm Point, Waddy Point, Wattle Point, Point Turner on Banksia Peninsula and Point Scott on Raymond Island. Each are cusped forelands of similar configuration, their western flanks showing evidence of erosion, yielding beach material which travels eastward, around the point, for deposition on prograding eastern shores. On Waddy Point Woodburn made repeated surveys which demonstrated the shoreward movement of a sand shoal from the lake floor on to the western shore. Progradation was only temporary, however, for the beach sands soon drifted round the point, to be added as a new beach ridge on the eastern shore (Fig. 3).

Such growth and migration of spits, accompanied by erosion of intervening bays, is the outcome of relatively strong wave action diagonally across the lake, especially from a westerly direction, and occasionally from the southeast. If it continues there will eventually be segmentation of Lake Victoria (Fig. 4), which has already been separated from Lake Wellington by a similar process of spit growth (Bird 1978).

Sand arriving from the west has enlarged the cusped foreland at Elbow Point, on the southern shore of Banksia Peninsula, since 1957, and on the northeast cor-

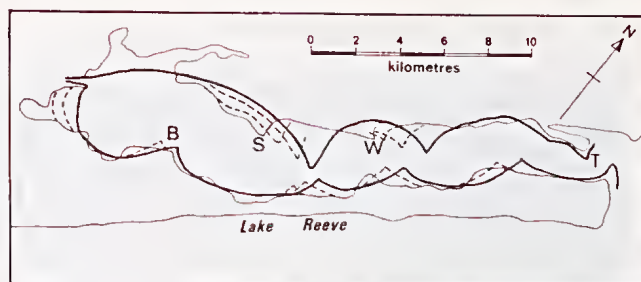


Fig. 4—Future segmentation of Lake Victoria may result from the growth and migration of bordering cusped spits and forelands. S—Storm Point, B—Beacon Point, W—Waddy Point, T—Turner Point.

ner of Sperm Whale Head sand eroded from the dune cliffs to the west and south has arrived to form a convergent spit, which has grown out from Point Wilson during this period.

LAKE KING

As in Lake Victoria, swampy shorelines already eroding in 1957 have continued to retreat, by up to 3.5 m, in the ensuing period. Erosion has been most rapid on the silty deltas of the Mitchell and Tambo Rivers. Bird and Rosengren (1971) traced stages in the reduction of the Mitchell delta from 266 hectares in 1848 to 178 hectares in 1940 and 145 hectares in 1970, and predicted its dissection into chains of silty islets by the year 2000. Between 1957-59 and 1982-83 erosion continued on this delta shoreline, with losses of up to 5 m locally, but in recent years the Public Works Department has stabilised much of the Mitchell delta by dumping granite and sandstone boulders along its more exposed shorelines (Figs 5, 6), and further dissection is now unlikely. However, it is possible that this armouring will cause deepening of the nearshore waters by reflected wave scour.

The breach that formed through the northern part of the delta, just downstream from Eagle Point Bluff, in 1919 is a deltaic crevasse that has persisted as 'The Cut'.

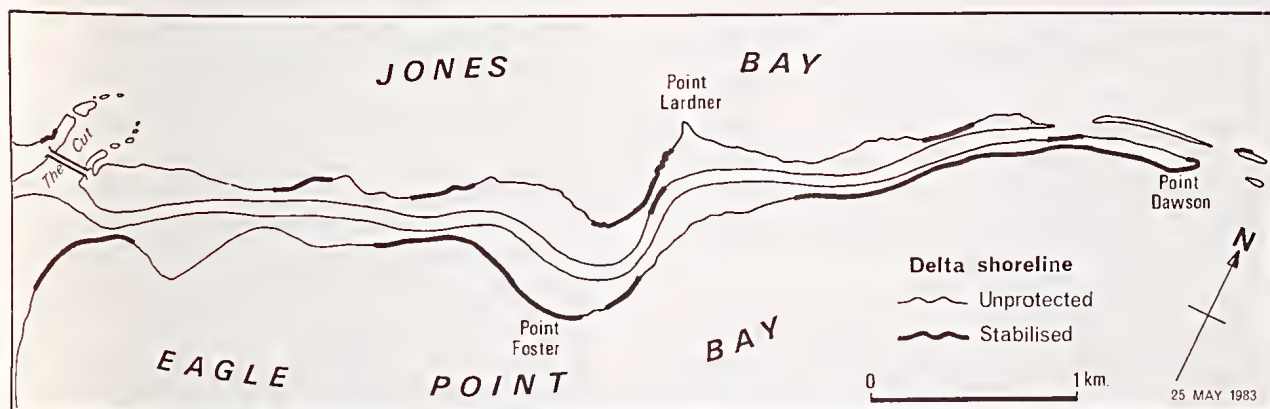


Fig. 5—Sectors of the shoreline of the Mitchell delta stabilised by the addition of boulder walls (as on 25 May 1983).



Fig. 6—Rapid shoreline erosion on the Mitchell delta has been halted by the dumping of granite and sandstone boulders to form a protective shoreline wall.
Photo: Eric C. F. Bird.

A minor deltaic feature has since grown out into Jones Bay as the result of deposition of sand, silt and clay washed down from the Mitchell River (Fig. 7). A lobate deposit has developed, the emerged parts of which carry rushes, sedges, and occasional *Phragmites* reeds, but fluvial sediment has not been trapped in the form of elongated jetties of the kind that developed the earlier Mitchell delta. This is because reedswamp no longer grows out in the shallow water of Jones Bay. In the absence of reedswamp, fluvial sediment has been more widely dispersed into Jones Bay, some of the sand having drifted along the northern shore of the Mitchell delta to accumulate as a beach on the western side of Point Lardner.

Erosion has continued on the northern shore of Jones Bay, especially near the mouth of the Nicholson River, and sand, drifting eastwards along the shore, has enlarged the spit which deflects the mouth of Salt Creek. Sand has also accumulated in the bays on either side of the Tambo delta, but this protruding silty delta has been further reduced by erosion along its lake shores and recession of river banks in the lower reaches (McRae-Williams *et al.* 1981, fig. 54). Since this delta was first surveyed in 1849 its area has been reduced by 11.2 hectares, of which 3.4 hectares were eroded between 1940 and 1977. Recession of the western shoreline since 1957-59 has been up to 30 metres, representing the greatest erosional change found in the Gippsland Lakes over this period, despite successive attempts to stabilise the shoreline with walls and groynes. However, as with the Avon and the Latrobe, sand is moving down the Tambo River, and in due course this is likely to become an area of shore sand accretion.

Swampy shorelines south of Eagle Point Bay and along the northern side of Raymond Island have receded by up to 3 m in the past 25 years, but erosion alongside McMillan Strait at Paynesville has been controlled by the building of shoreline walls.

Locally there has been sand accretion on beach-fringed sectors around Lake King since 1957-59.

Beaches have been widened at and north of Tambo Bluff and in the bay north of Jubilee Point, while the spit at Point Jones has been enlarged by the accumulation of sand washed in from the lake floor. East of Point Jones, swampy shorelines have been cut back, particularly on the more exposed sectors, which have retreated by more than 2 m since 1957-59. At Metung the west-facing beach has been augmented artificially by dumping sand dredged from the Tambo River to offset earlier erosional losses (R. Bull, pers. comm.). Some of this sand has drifted south to be added to the end of Shaving Point, and there has also been sand accretion on the shore of the Boole Boole Peninsula east of Metung.

South of Lake King the Bunga Arm is a long, narrow lagoon behind the dune-covered outer barrier and the Ninety Mile Beach. In general these dunes are held in place by a dense cover of scrub and woodland vegetation, but a sector about 10 km east of Ocean Grange has been modified by the growth of a blowout which has delivered wind-blown sand to the lagoon shoreline, resulting in the formation of sandy beaches, spits and cusped forelands. A wide triangular fan of sandy sediment now extends half way across the lagoon at this point. In 1957-59 sand was still being blown into the Bunga Arm here, but subsequently the dunes have become covered by marram grass and stabilised. The sand supply to Bunga Arm has thus almost ceased, and the beaches, spits and cusped forelands are no longer growing. However, they are still being re-shaped by wave action, and eventually they could grow in such a way as to produce segmentation of Bunga Arm.

In the eastern part of Lake King, between Metung and Lakes Entrance, shoreline changes have been generally slight. Erosion of swamp land has continued at the mouth of Chinaman Creek, near Metung, and along the lake shore south of Flannagan Island, but there has been some sand accretion on the spits bordering Flannagan Island. Sand dredged from the lake floor to maintain navigable channels has been dumped to reclaim marshland and shallow embayments on Rigby Island



Fig. 7—The spatulate pattern of accretion outside The Cut, a gap through the northern arm of the Mitchell River delta, as the result of the deposition of fluvial outwash in Jones Bay. Most of the deposition is underwater, but minor deltaic formations have developed at A and B, marking local progradation of the shoreline.

Photo: Neville Rosengren.

and to create new land on and around Bullock Island, near Lakes Entrance. The use of such sand to fill bays and marshes and form lake-shore beaches should be preceded by an environmental impact assessment, for it could have ecological effects, particularly where the dumped material obliterates salt marsh vegetation or nearshore *Zostera* beds, thereby modifying habitats for fish and bird life.

Cunningham Arm, at and east of Lakes Entrance, has been changed since 1957-59 by the extension of sea walls along its northern shore, and by the eastward migration of sand spits and cusped forelands along its southern shore (Fig. 8). As in Bunga Arm, these sandy formations were being nourished in 1957-59 by wind-blown sand spilling across the outer barrier at several points. Previously, the accumulation of such sandy material at the eastern end of Cunningham Arm had

reduced and segmented the formerly navigable waterway (Reeve River) that led to the variable, migratory natural outlet from the Gippsland Lakes before the present artificial entrance opened in 1889 (Bird & Lennon 1973, Miles 1977). In the nineteen-sixties, planting of marram grass by the Soil Conservation Authority stabilised the dunes on the outer barrier and reduced the sand spillover into Cunningham Arm. As a result the beaches and spits on the southern shore of Cunningham Arm were no longer nourished by this process.

The scalloped southern shore of Cunningham Arm, with its eastward-drifting spits (Fig. 9), has shown little net change since 1957, but the distribution of sand has been modified. In recent years a new source of sand has been produced by the dumping of dredged material on the southern shore opposite the township of Lakes Entrance, and this is being carried eastwards by longshore drifting. It is likely that the sandy material thus provided will eventually accumulate east of the footbridge, shallowing and shrinking Cunningham Arm. Such changes are likely to be resented by people who now use Cunningham Arm for fishing and water-borne recreation, and by those who would wish to retain this lagoon as a scenic feature in the environment of Lakes Entrance.

LAKE REEVE

Lake Reeve is an elongated lagoon between the inner and outer barriers south-west from Sperm Whale Head. Its eastern part is a branch of the Gippsland Lakes which shallows rapidly south-westwards, much of it being generally a dry muddy sandflat, submerged only after heavy rains, or when easterly winds or river flooding raise the water level in the southern part of Lake King, driving water south-westwards. Salt marshes dominated by *Salicornia* spp. are extensive around its shores, many sectors of which are bordered by low, parallel beach ridges, typically up to 20 cm high and spaced at intervals of up to 60 m.

Shoreline surveys in 1957-59 were less detailed in Lake Reeve, but comparison of air and ground photographs taken during that period with the present configuration shows that on some sectors up to three new beach ridges have been formed, representing an advance of the shoreline of up to 10 m in this period. The pattern is too intricate to be included in Fig. 1. Observa-

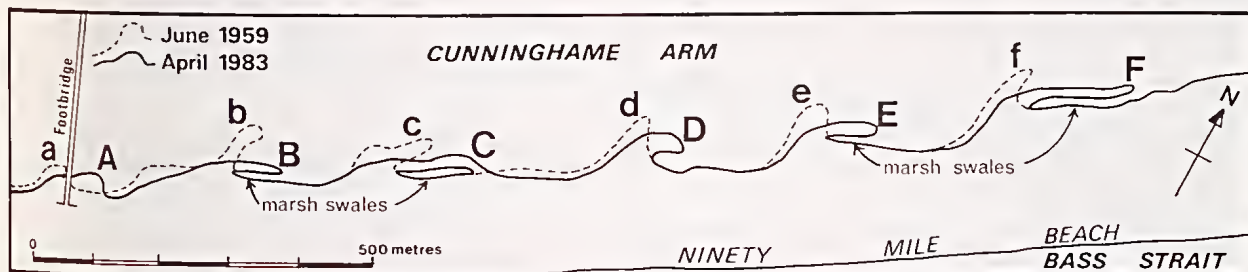


Fig. 8—Comparison of surveys of the sandy southern shoreline of Cunningham Arm in 1959 and 1983 show that cusped spits have moved eastwards (a—A, b—B, etc.) and developed longer, flatter alignments, in some cases enclosing small salt marsh swales.



Fig. 9—The southern shoreline of Cunninghame Arm, Lakes Entrance, looking eastward to Red Bluff. Sand spits, formerly nourished by dunes spilling over the enclosing barrier (especially at X), and now augmented by dredged sand dumped on the shore (Y), are migrating eastwards. A to F are the features shown in Fig. 8.

Photo: Eric C. F. Bird.

tions in recent years have shown that the beach ridges form during phases when Lake Reeve is occupied by water for periods of several months (as in 1971). Wave action, chiefly from westerly directions, then washes sand, silt, and the abundant small shells (mainly *Coxiella striata*) up on the margins of the lake, lodging them against the edge of the salt marsh vegetation. When the lake dries out, wave action ceases and the ridges become stable features. Vegetation then colonises them, and *Salicornia* spreads forward from the newly-formed ridge, forming a new salt marsh fringe. When Lake Reeve is next awash, another beach ridge may be added at the salt marsh edge, some distance in front of its predecessor (Fig. 10).

As a result of this recurrent beach ridge formation, Lake Reeve has been reduced in area. For this reason the ridges have been termed contraction ridges (Bird 1978), although they have also been called 'mini-cheniers' (Davis *et al.* 1977) on the grounds that they formed on a marshy foundation. The pattern of these ridges varies

along the shores of Lake Reeve, some sectors having advanced more rapidly to form forelands which may eventually coalesce, segmenting this lagoon. However, intermittent wave action in Lake Reeve, compared with perennial lagoons such as Cunninghame Arm, renders this a very slow process.

DISCUSSION

Although the surveys carried out in 1957-59 were intended only to detect shoreline changes in progress at that time, they have provided a basis for determining the pattern of change around the Gippsland Lakes in the ensuing quarter-century (Fig. 1). The changes have been less than the author would have predicted in 1959. This is partly because some sectors of the lake shoreline have been stabilised artificially, but two other factors are relevant. First, much of the shoreline change has taken place during occasional stormy periods or episodes of flooding. In 1957-59 the lakes' shoreline showed many features that had developed during the severe floods in 1952, notably erosion scars that then suggested a relatively rapid rate of shoreline recession. Although there have been subsequent floods, notably in 1971 and 1978, and a number of stormy periods, the past 25 years may not have been as boisterous as the preceding 25 years, which included major episodes of river flooding in 1934, 1949, 1951, 1952, and 1953. Second, there has been a marked change since 1957-59 in the extent of water weeds, notably *Zostera* spp., in the shallow near-shore waters of Lake Victoria and Lake King. In the nineteen-fifties there was very little *Zostera* growth in these lakes, possibly because of the presence of vast numbers of crabs (*Paragrapsus* spp.), but since the early nineteen-sixties the crab population has diminished and *Zostera* growth has become extensive and luxuriant. Wave action is much reduced in sectors where *Zostera* is present, and the increase in this weed growth has un-

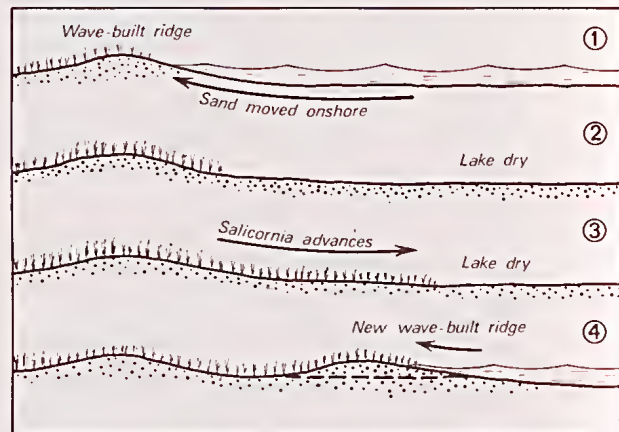


Fig. 10—Evolution of wave-built sandy beach ridges on the shores of Lake Reeve is related to episodes of high lake level, alternating with phases when the lake dries out, and vegetation (mainly *Salicornia*) spreads forward to set the scene for the next beach ridge formation.

doubtedly slowed down erosion on the lake shoreline in the past two decades.

Geomorphological studies in 1957-59 (Bird 1978) emphasised the role of shore-line reedswamp in promoting silt accretion in the Gippsland Lakes, and identified the loss of much of the former reedswamp fringe as the main reason for widespread shoreline erosion, especially on swampy sectors. During the past 25 years, there has been further reedswamp reduction, and consequent onset of shoreline erosion, particularly in Lake Wellington. However, many of the changes that have occurred on the shoreline of the Gippsland Lakes in the past 25 years are the result of sand movement alongshore and across lake floors, particularly from west to east, and its accumulation on spits and forelands, west-facing shores and embayments.

In contemplating the changes that may occur in the next 25 years, the significance of sand moving down the rivers, especially the Latrobe, the Avon, and the Tambo, must also be considered. If there is frequent and severe river flooding during this period, these rivers will be delivering sand to the lakes, and shoreline sectors now swampy and eroding will become fringed by sandy beaches. It seems likely that within the next century the eroding silty deltas of these rivers will give place to growing sandy deltas. Meanwhile, the modern enthusiasm for dumping sand dredged from navigation channels and from rivers on sectors of the lake shore could accelerate this increase in sandiness on the shorelines of the Gippsland Lakes.

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STUDIES ON WESTERN AUSTRALIAN PERMIAN BRACHIOPODS

3. THE FAMILY LINOPRODUCTIDAE STEHLI 1954

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ABSTRACT: Representatives of the Linoproductidae (Productida, Brachiopoda) from the Western Australian Permian sequences are documented. Species are assigned to *Linoproductus*, *Cancrinella*, and *Lyonia* gen. nov. within the Linoproductinae and to *Globiella* within the Stepanoviellinae. The following species are revised or described: *Linoproductus* sp., *Cancrinella irwinensis* sp. nov., *Cancrinella bella* (Etheridge), *Cancrinella coolkilyaensis* sp. nov., *Cancrinella* sp. A, *Cancrinella* sp. B, *Lyonia lyoni* (Prendergast), *Globiella umariensis* (Reed), *Globiella foordi* (Etheridge), *Globiella flexuosa* (Waterhouse). The classification of the family Linoproductidae is briefly discussed and the Proboscideolinae of Muir-Wood and Cooper is raised to family status as the Proboscideallidae.

This paper reviews and describes all known Western Australian Permian species of the Linoproductidae. Representatives of *Cancrinella* and *Globiella* are particularly abundant at certain stratigraphical levels and are useful for intrabasinal correlations.

COLLECTIONS AND TERMINOLOGY

Figured and measured specimens are housed in the institutions indicated by the following prefixes to registered numbers. CPC—Commonwealth Palaeontological Collections of the Bureau of Mineral Resources, Geology and Geophysics, Canberra; GSWA—Geological Survey of Western Australia, Perth; AMF—Australian Museum, Sydney; MUGD—Department of Geology, University of Melbourne; UWA—Department of Geology, University of Western Australia, Perth. The terminology used herein follows Muir-Wood (1965) and Sarycheva (1970).

STRATIGRAPHY AND AGE

Marine Permian sedimentary sequences in the Perth, Carnarvon and Canning Basins each contain Linoproductidae; their biostratigraphy and lithostratigraphy have been alluded to previously (Archbold, 1981, 1982a).

SYSTEMATIC PALAEONTOLOGY

Order PRODUCTIDA Sarycheva & Sokolskaya 1959

Suborder PRODUCTIDINA Waagen 1883

Superfamily LINOPRODUCTACEA Stehli 1954

Family LINOPRODUCTIDAE Stehli 1954

DIAGNOSIS: Normally costellate Linoproductacea, rarely rugose, row of fine spines near hinge, cardinal process trilobate, small body cavity, dendritic, striate or smooth ventral adductor scars.

DISCUSSION: The classification of the Linoproductacea presented by Waterhouse (1978a), is provisionally accepted with minor modification. Wang *et al.* (1966) anticipated several of the modifications suggested by Waterhouse (1978a) and I formally raise the Proboscideolinae Muir-Wood & Cooper 1960 to the family

Proboscideallidae. The family is characterised by the distinctive morphology of the ventral valve and the bilobate cardinal process of the two included genera: *Proboscideella* Oehlert 1887 and *Siphonosia* Cooper & Grant 1975. As in Waterhouse (1978a), the Giganoproductidae are provisionally included within the Linoproductacea because genera such as *Linoprotonia* Ferguson 1971 and species groups such as the *Giganoproductus maximus* group (Pattison 1981) appear to be linoproductaccan in affinity. The Linoproductidae is restricted to include the Linoproductinae, Stepanoviellinae and the Yakovleviinae. The latter, which includes *Yakovlevia* Fredericks (1925) and *Duartia* Mendes (1959) is retained within the Linoproductidae in view of their trilobate cardinal process and finely costellate ornament.

Subfamily LINOPRODUCTINAE Stehli 1954

DIAGNOSIS: Linoproductidae with dendritic or striate ventral adductor scars, wide hinge and trail usually long.

GENERA INCLUDED AND DISCUSSION: The following genera are included in the subfamily: *Linoproductus* Chao 1927, *Cancrinella* Fredericks 1928, *Terrakea* Booker 1930, *Marginirugus* Sutton 1938, *Haydenella* Reed 1944 (see Grant, 1976), *Fluctuaria* Muir-Wood & Cooper 1960, *Ovatia* Muir-Wood & Cooper 1960, *Grandaurispina* Muir-Wood & Cooper 1960, *Balakhonia* Sarycheva 1963, *Asperlinus* Waterhouse & Piyasin 1970, *Striatospica* Waterhouse 1975, *Auriculispina* Waterhouse 1975, *Vitilipproductus* Ching & Liao 1974, *Magadania* Ganelin 1977 (in Grigor'eva *et al.* 1977), *Kasetia* Waterhouse 1981 and *Lyonia* gen. nov. The genera *Holotricharina* Cooper & Grant 1975 and *Undellaria* Cooper & Grant 1975, included by those authors in Linoproductinae, are only provisionally retained within the subfamily. Both Texan genera are characterised by a non-costellate external ornament and hence are not "conventional" Linoproductinae.

Discussion of *Haydenella* Reed by Grant (1976) indicates a firm linoproductinid affinity for the genus contrary to the view of Jing and Hu (1978), who also synonymised *Chianella* Waterhouse (1975) with *Haydenella* Reed (1944).

Auriculispina Waterhouse (1975), type species *Cancrinella levis* Maxwell (1964) from the Asselian Burnett Formation, Yarrol Basin, Queensland, requires further investigation (Waterhouse 1976a); the genus is assigned provisionally to the Linoproductinae.

Genus *Linoproductus* Chao 1927

(= *Cora* Fredericks 1928; = *Euproductus* Whitehouse 1928)

TYPE SPECIES: *Productus cora* d'Orbigny 1842.

DIAGNOSIS: The diagnosis provided by Muir-Wood and Cooper (1960) is used herein.

Linoproductus sp.

Fig. 1A, B

MATERIAL: One internal mould of a ventral valve, GSWA11192, from GSWA locality 30111. Mt. Phillips (1972) run 6/1212, pt. 1117 RMH, BK5, Lyons Group, Yard Grid 360-937 of Tastubian (Early Sakmarian) age.

DESCRIPTION: Specimen transversely oval in outline. Ventral valve unevenly convex with posterior strongly curved and anterior of valve gently curved. Ventral umbo small, pointed. Rugae distinctly developed on ears and extremities of lateral slopes but not crossing venter. Surface finely costellate, with 27 costellae per cm at 1.5 cm from umbo and 16 costellae per cm at 3 cm from umbo. Anterior of valve turned into trail.

DISCUSSION: The fine costellae, some bifurcating, others arising from intercalation, the arrangement of the rugae and the large size (height = 34 mm; maximum width = 44 mm) suggest a species of *Linoproductus*. The specimen is differentiated from *Globiella* by its finer costae and the convexity of the ventral valve. Material is inadequate for comparison with other species of the genus but this specimen appears to be the only *Linoproductus* known from the Permian of Australia.

Genus *Cancrinella* Fredericks 1928

TYPE SPECIES: *Productus cancrini* de Verneuil 1845.

= *Productus cancrini* de Verneuil 1842 (in de Koninck 1842).

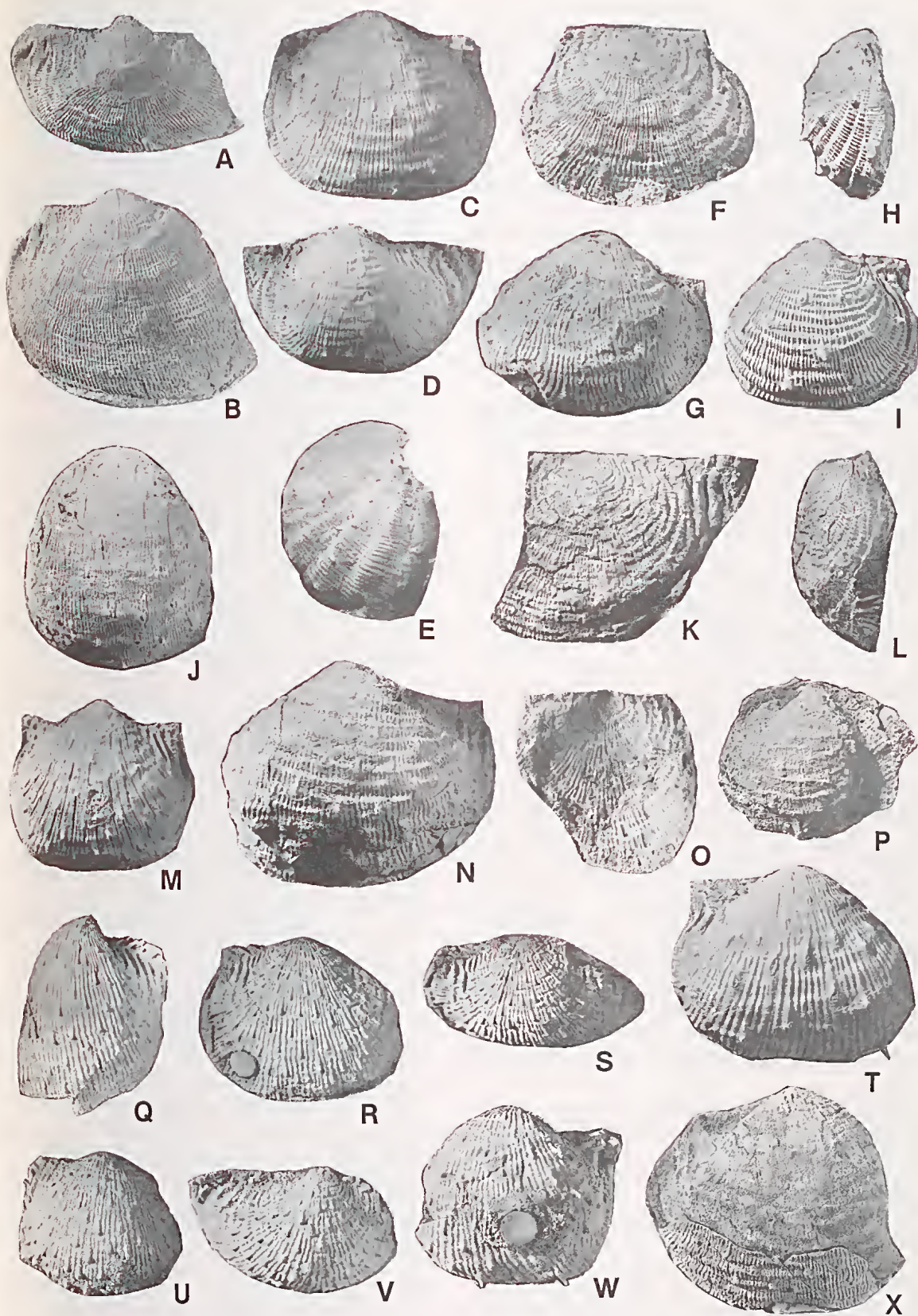
DIAGNOSIS: Small to medium, thin shelled Linoproductinae with small, flattened ears and strongly incurved umbo. Ventral valve with fine costellae and numerous long fine spines arising from costellae at a low angle; tuft of halteroid spines developed on ears. Dorsal valve costellate and rugose, dimpled with no spines. Ventral valve with rugae—at times only on ears.

DISCUSSION: Hill (1950) and Muir-Wood and Cooper (1960) discussed the early usage of *Productus cancrini*—first by de Koninck (1842) who figured a Lower Carboniferous shell, then by de Verneuil and Murchison (1844) in a list of Permian fossils of Europe and finally, in a restricted sense, by de Verneuil (1845, in, Murchison *et al.*, 1845) for the Permian shells; the Carboniferous shells of de Koninck were transferred to *Productus koninckianus* de Verneuil (1845 in Murchison *et al.*, 1845). I follow Cooper and Grant (1975) and Grigor'eva *et al.* (1977) and regard the type species of *Cancrinella* as being *Productus cancrini* de Verneuil (1845). As noted by Hill (1950, p. 12), de Verneuil (1845) in effect chose

de Koninck's (1842) Russian Zechstein specimen as the lectotype when he renamed the Viséan specimens *P. koninckianus*. This stabilised the character and horizon of *P. cancrini*, if not the author, but Fredericks (1928) chose *P. cancrini* de Verneuil (1845) as the type species of his genus. To stabilise authorship of *P. cancrini*, Fredericks's choice should be regarded as being a clear indication that he intended the Permian species to be type. De Koninck (1842), Table opposite p. 154) stated that de Verneuil was the author of *Productus cancrini* although on page 180 he attributed the name to both de Verneuil and von Keyserling. As a result 1842 could justifiably be given as the date of de Verneuil's species.

Grigor'eva *et al.* (1977) recognised two species groups within *Cancrinella*, namely the group of *C. cancrini* (de Verneuil) and the group of *C. cancriniformis* (Tschernyschew 1889). *Cancrinella cancrini* (de Verneuil) is a variable species (Grigor'eva *et al.* 1977, pl. 19, figs 1-9) lacking rugae on the ventral valve, except on the small ears, and possessing well spaced spines which are relatively coarse as in other species assigned to the group. The group of *C. cancriniformis* possesses distinct rugae across the ventral valve and strongly developed rugae on the ears. Spines in this group may be finer and more regularly spaced. The two groups are not mutually exclusive. *Cancrinella bella* (Etheridge 1918), is an intermediate, and it appears unwise to formalise the two groups. Large species attributed to *Cancrinella* (e.g. *C. grandis* Solomina 1981) that possess dorsal valve spines are not true representatives of the genus and are not morphologically close to the species described below nor to *C. cancrini* and its allies from European Russia. Such species may be better referred to either *Filiconcha* Dear 1969 or *Cancrinelloides* Ustritskiy (in Ustritsky & Chernyak 1963)—both genera apparently being allied to the Monticuliferidae (see Waterhouse 1976a).

Fig. 1—A-B, *Linoproductus* sp.; from Lyons Group, Carnarvon Basin, A-B, GSWA11192, ventral valve internal mould in posterior and ventral views, $\times 1$. C-P, *Cancrinella irwensis* sp. nov.; C-G, J, M from Fossil Cliff Member, Perth Basin; H-I, K-L, N-O, from Callytharra Formation, Carnarvon Basin, P, from Cuncudgerie Sandstone, Canning Basin. C-E, Holotype, CPC19915A, ventral valve internal mould in ventral posterior and lateral views, $\times 1.3$, $\times 1.5$ and $\times 1.3$ respectively. F, CPC199151, dorsal valve external mould, $\times 1.5$. G, CPC19915F, ventral valve internal mould in ventral view, $\times 1.5$. H-I, MUGDF6027, ventral valve in lateral and ventral views, $\times 1.5$. J, CPC19915B, ventral valve internal mould in ventral view, $\times 1$. K-L, CPC19917C, dorsal valve in ventral and lateral views, $\times 1.2$. M, CPC19915G, ventral valve internal mould in ventral view, $\times 1.4$. N, CPC19917B, ventral valve in ventral view, $\times 1.2$. O, CPC19917F, dorsal valve in dorsal view, $\times 1.5$. P, CPC19918, natural cast of ventral valve in ventral view, $\times 1.3$. Q-X, *Cancrinella bella* (Etheridge); Q-S, U-X, from Noonkanbah Formation, Canning Basin; T, from Wandagee Formation, Carnarvon Basin. Q, AMF16812, ventral valve in ventral view, $\times 1.3$. R-S, AMF16731, ventral valve in ventral and posterior views, $\times 1.3$. T, MUGDF6028, ventral valve in ventral view, $\times 1.8$. U-V, AMF16734, ventral valve in ventral and posterior views, $\times 1.3$ and $\times 1.5$ respectively. W, AMF16742, lectotype, ventral valve in ventral view, $\times 1.3$. X, CPC19919, ventral valve in ventral view, $\times 1$.



Cancrinella irwinensis sp. nov.

Fig. 1C-P

- 1890 *Productus undatus*: Foord. *Geol. Mag. Dec.*, 3(7): 152, pl. 7, fig. 6.
 1907 *productus undatus*: Etheridge. *Bull. geol. Surv. W. Aust.*, 27: 30.
 1910 *Productus undatus*: Glauert. *Bull. geol. Surv. W. Aust.*, 36: 87.
 1926 *Productus bellus*: Glauert (*partim.*) *Bull. geol. Surv. W. Aust.*, 88: 46.
 1931 *Productus undatus*: Hosking. *J. roy. Soc. W. Aust.*, 17: 8, 22.
 1935 *Linoproductus cancriniformis*: Prendergast (*partim.*), p. 14, pl. 2, figs 7-10. *non. cet.*).
 1943 *Linoproductus cancriniformis*: Prendergast (*partim.*), p. 23.
 1957 *Linoproductus cancriniformis*: Coleman (*partim.*), p. 69.
 1957 *Linoproductus lyoni*: Coleman (*partim.*), p. 76.

ETYMOLOGY: From the Irwin River, Perth Basin, Western Australia.

HOLOTYPE: CPC19915A, a ventral valve internal mould from BMR Locality IR20, Fossil Cliff Member, Perth Basin.

MATERIAL AND LOCALITIES: CPC19915A-199151, 8 ventral valve internal moulds and 1 dorsal valve external mould from BMR locality IR20, Carynginia Gully, 2.8 km on a bearing of 297° from Carynginia Well, Fossil Cliff Member; CPC19916A-19916C, 2 ventral valve internal moulds and 1 dorsal valve external mould from BMR locality PB7, 0.8 km on a bearing of 334° from Carynginia (No. 1) Well, Irwin River Area, Fossil Cliff Member, Perth Basin; CPC19917A-19917F, 4 ventral valves and 2 dorsal valves from BMR locality 7044/0116, Minilya Run 13A Photo 5043, JMD Pt. 1, middle part of Callytharra Formation; MUGDF6027, a ventral valve from G. A. Thomas locality P491, 33 m above base of type section of Callytharra Formation, Callytharra Springs, Carnarvon Basin; CPC19918, natural cast of ventral valve from BMR locality T0127, Scott Bluff, Lake Blanche, 22°31'06"S, 124°14'16"E, Cuncudgerie Sandstone, Canning Basin.

DIAGNOSIS: Medium to large sized *Cancrinella*. Normally with strongly convex ventral valve. Strongly, but finely, rugose and costellate shell with fine spines on ventral valve. Dorsal valve relatively weakly geniculate.

TABLE 1
SIZE RANGES OF POPULATIONS OF *Cancrinella irwinensis* sp. nov.
(in mm)

Stratigraphic horizon	Maximum width	Hinge width	Ventral length	Dorsal length	Thickness
Fossil Cliff	18.0-32.0	14.2-22.5	15.5-33.1	17.7	8.8-19.2
Callytharra	18.5-39.0	18.2-38.0	16.1-29.0	14.0-28.0	13.8-14.5
Cuncudgerie	17.3	—	18.0	—	—

DESCRIPTION: Medium to large for genus, subquadrate to elongate outline. Maximum width slightly greater than hinge width. Shell surface marked by distinct, fine rugae and costellae. Rugae strongest on ears and lateral slopes, distinct but low across venter and trail. Costellae rounded with narrow interspaces, number about 2 to 3 per mm at 1.5 cm from ventral umbo. Rugae number 12+ in first cm of growth and about 6 in second cm of growth. Spines arranged in tufts on ears, body spines arise from end of elongate swollen costellae, extend anteriorly at a low angle to shell surface. Dorsal valve with costellae, fine rugae and elongate dimples.

Profile of ventral valve strongly convex, trail slightly less curved than posterior of valve. Ventral umbo small, overhangs dorsal umbo. Ears distinct, square in outline.

Dorsal valve gently concave in region of visceral disc, relatively weakly geniculate on trail. Trail at about 20°-50° to plane of visceral disc (see also Prendergast 1935, pl. 2, fig. 7).

Ventral interior may carry extensive elongate narrow ridges (specimen CPC19915G, Fig. 1M) over entire visceral disc. Dorsal interior poorly known; small cardinal process and distinct median septum present.

DISCUSSION: Coleman's (1957) three examples of *Linoproductus lyoni* from the Callytharra Formation were examined and found to be variably preserved specimens of the new species.

Rare specimens from the Callytharra Formation with the characteristic ornament of the species indicate a maximum width probably in excess of 50 mm. They are invariably distorted and crushed but appear to be somewhat less convex than smaller specimens.

C. irwinensis belongs to the *C. cancriniformis* group with distinct rugae across the venter of the shell. *C. cancriniformis* possesses somewhat coarser rugae than the present species and more pronounced ears. Species allied to *C. cancriniformis* from the Early Permian of Siberia (Zavodovsky & Stepanov 1971) are insufficiently known for detailed comparison. The *C. altissima* King of Grunt and Dmitriev (1973) from the Sakmarian of the Pamirs is a small species, with distinct fine rugae, that is close to juvenile specimens of *C. irwinensis*. *C. cancriniformis* from the Late Sakmarian or Early Artinskian of southern Thailand (Waterhouse 1981) is close to *C. irwinensis* in details of costellae and rugae but the overall shell shape of the Thai species is not well known.

Eastern Australian Permian species of *Cancrinella* such as *C. magnifica* Campbell 1953 and *C. gyrandensis* Wass 1966 are large, coarsely rugose species not closely related to West-Australian representatives of the genus. *Cancrinella farleyensis* (Etheridge & Dun 1909, pl. 42, figs 9-11; Reid 1929, p. 83, fig. 37.4; McClung 1980, fig. 7) is also large but has weaker rugae and finer costellae than other eastern Australian species. New Zealand Permian species are close to eastern Australian representatives of the genus (Waterhouse, 1964, 1982a).

AGE AND STRATIGRAPHIC RANGE: Fossil Cliff Member, Perth Basin; Callytharra Formation, Carnarvon Basin; Cuncudgerie Sandstone, Canning Basin; Sterlitamakian (Late Sakmarian).

Cancrinella bella (Etheridge 1918)

Figs 1Q-X, 2A, B

1918 *Productus bellus* Etheridge, p. 254, pl. 39, figs 4, 5; pl. 40, fig. 6.1926 *Productus bellus* Etheridge; Glauert (*partim.*) *Bull. geol. Surv. W. Aust.*, 88: 46.1935 *Linoproductus cancriniformis*: Prendergast (*partim.*), p. 14, pl. 2, figs 11-12 (non. *cet.*).1943 *Linoproductus cancriniformis*: Prendergast (*partim.*), p. 23.1957 *Linoproductus cancriniformis*: Coleman (*partim.*), p. 40-69, pl. 8, figs. 2-9 (non. *cet.*).

LECTOTYPE: Ventral valve, AMF16742, figured by Etheridge (1918, pl. 39, fig. 5) herein selected.

MATERIAL AND LOCALITIES: Etheridge's (1918) syntypic series of 4 ventral valves and 1 dorsal valve from Mt. Marmion, Noonkanbah Formation, Canning Basin was reexamined. CPC19919, a ventral valve, from BMR locality KNF76, type section of Noonkanbah Formation, 6.8 km at 298° from Bruten's Old Yard, Cherabun Station, about 400 m above base of section. MUGDF6028, a ventral valve from a generalised collection labelled "Calceolispongia bed, east limb of syncline at Minilya River", collector C. Teichert, Wandagee Formation, Carnarvon Basin.

DIAGNOSIS: Small to medium sized *Cancrinella*. Moderately convex ventral valve. Rugae strongly developed on ears but weak to absent across venter. Costellae distinct, coarse. Dorsal valve flat on visceral disc, distinctly geniculate.

DESCRIPTION: Species small to medium sized, sub-quadrate to rounded in outline. Maximum width slightly greater than hinge width. Shell surface marked by distinct, concentric rugae on ears and posterior extremities of the flanks. Rugae absent or very weakly developed across venter. Large gerontic ventral valve (Fig. 1X) has distinct, relatively fine, rugae anteriorly. Costellae well developed, rounded with narrow interspaces, about 1 to 1.5 per mm at 1.5 cm from the umbo, and relatively coarse. Spines arranged in strong tuft of two rows on ears, body spines arise from anterior end of elongate, swollen costellae and extend anteriorly at low angle to shell surface. Body spines relatively dense and arranged in quincunx. Dorsal valve exterior with elongate dimples, costellae and wrinkles, the latter only developed prominently on ears.

Profile of ventral valve convex; no specimen has a marked trail. Ventral umbo small, overhangs dorsal umbo. Ears distinct, usually pointed.

Dorsal valve flat in region of visceral disc, distinctly geniculate on trail. Dorsal interior with normal *Cancrinella* type cardinal process and thick, strong septum approximately two-thirds of valve length. Low, broad marginal ridge extends around posterior of visceral disc.

Ventral interior unknown.

DISCUSSION: *Cancrinella bella* is distinguished from *C. irwinensis* by its less strongly convex ventral valve, coarser costellae, concentric rugae that are absent or only weakly developed on the venter except in old age,

distinctly geniculate dorsal valve, and more closely spaced spines. *C. bella* is closer to *C. coolkilyaensis* sp. nov. in details of ornament but has a less strongly convex ventral valve and weaker, finer rugae on the ears and lateral slopes.

The coarser costellae, and lack of well defined rugae on the venter of smaller representatives of *C. bella* recalls the external appearance of species such as *C. singletoni* Gobbett 1964 from the Upper Wordiekammen Limestone, Bunsow Land, Spitzbergen and *C. crassa* Gobbett 1964 from the *Cyathophyllum* Limestone, Spitzbergen. Gobbett's species belong to the group of *C. cancrini* and tend to have even more poorly developed rugae on their ears than those of *C. bella* and also tend to be more strongly convex ventrally. Spine bases on *C. singletoni* are coarser than those of *C. bella*.

C. bella was included, with specimens now attributed to *C. irwinensis*, in *Linoproductus cancriniformis*, (Prendergast 1935, 1943, Coleman 1957). Coleman (1957, pl. 8, figs 2-9) figured several specimens from the Wandagee Formation that can confidently be attributed to *C. bella* on the basis of relatively coarse costellae and ill defined to absent rugae over the venter.

AGE AND STRATIGRAPHIC RANGE: Noonkanbah Formation, Canning Basin; Wandagee Formation, Carnarvon Basin. Late Baigendzinian (Latest Artinskian).

Cancrinella coolkilyaensis sp. nov.

Fig. 2C-O

1957 *Linoproductus cancriniformis*: Coleman (*partim.*), p. 69, pl. 8, fig. 1 (non. *cet.*).

ETYMOLOGY: From Coolkilya Paddock on Wandagee Station.

HOLOTYPE: CPC19920A, a ventral valve internal mould from the Coolkilya Greywacke, Carnarvon Basin.

MATERIAL AND LOCALITIES: CPC19920A-19920G, 4 internal moulds of ventral valves, 1 external mould of a ventral valve, 1 incomplete internal mould of a conjoined shell and 1 external mould of a dorsal valve all from BMR locality ML79, 2.4 km south east of Trig. Point on Wandagee Hill, Coolkilya Greywacke, Carnarvon Basin. UWA88109-88111, 3 internal moulds of ventral valves from UWA L12, *Linoproductus* section east of Wandagee Hill, Nalbia Paddock, horizon 1, collector C. Teichert, now in Coolkilya Greywacke.

DIAGNOSIS: Medium sized *Cancrinella*. Strongly convex ventral valve. Weakly rugose shell with low rugae extending across venter. Spines relatively fine and costellae relatively coarse. Ears and lateral slope extremities coarsely rugose. Dorsal valve strongly geniculate.

DESCRIPTION: Species medium-sized for genus, elongate in maturity with straight sides. Maximum width greater than hinge width. Shell surface marked by concentric rugae, coarse and distinct on ears and extremities of lateral flanks and weakly present across venter of shell. Rugae stronger on trail of ventral valve. Costellae rounded with narrow interspaces, about 1 to 1.5 per mm at 1.5 cm from ventral umbo. About 5 rugae per cm in

TABLE 2

MEASUREMENTS OF *Cancrinella coolkilyaensis* sp. nov. (in mm)

* = holotype; e = estimate; † = incomplete specimen

Specimen number	Maximum width	Hinge width	Ventral length	Dorsal length	Thickness
UWA88109	23.6	19.0e	28.2	—	18.6
UWA88110	23.0†	—	—	—	—
UWA88111	19.4†	—	—	—	—
CPC19920A*	25.0	—	23.2	—	14.1
CPC19920B	22.2	25.0e	21.0e	—	11.2
CPC19920C	20.2	19.0	—	—	—
CPC19920D	—	—	13.0e	—	—
CPC19920E	—	—	16.5†	13.5e	—
CPC19920F	26.0	—	—	15.3	—

the second cm of growth. Spines arranged in tuft of two rows on ears; body spines, only slightly wider than costellae, arise from anterior extremities of elongate, somewhat swollen costellae, extend anteriorly at low angle to shell surface. Dorsal valve distinctly rugose over visceral disc, strongly rugose on trail with strong costellae and elongate dimples.

Profile of ventral valve strongly convex, with convexity of trail being less than that of posterior of valve. Ventral umbo small, overhangs dorsal umbo. Ears distinct, pointed in outline.

Dorsal valve flat on visceral disc, strongly geniculate anteriorly, initially at 70°–80° and anteriorly up to 120° from plane of visceral disc.

Ventral interior may carry numerous elongate narrow ridges over visceral disc of valve (specimen CPC19920A). Dorsal interior poorly known, traces of delicate median septum occur on specimen CPC19920E.

DISCUSSION: *Cancrinella coolkilyaensis* is distinguished from *C. irwinensis* by its coarser costellae, weaker rugae and strongly geniculate dorsal valve. *C. bella* is closer to *C. coolkilyaensis* but possesses a less convex ventral valve, and possibly a less geniculate dorsal valve in addition to a lacking or having weak rugae over the venter of specimens of comparable size; its dorsal valve has weaker rugae. The new species is close to *Cancrinella* sp. (Archbold 1982b) from Late Baigendzinian/Early Kungurian black shales of Irian Jaya in terms of ventral convexity and development of rugae. The Irian Jaya species, however, possesses finer costellae than *C. coolkilyaensis*.

AGE AND STRATIGRAPHIC RANGE: Coolkilya Greywacke, Carnarvon Basin. Middle Kungurian.

Cancrinella sp. A

Fig. 2P–R

MATERIAL AND LOCALITIES: CPC19921A–C, 1 internal mould of a dorsal valve, 1 external mould of a dorsal valve and 1 internal mould of a ventral valve all from BMR locality GW54, 7.6 km from Dairy Creek Homestead on bearing of 115°, on south bank of Bush Creek, Coyrie Formation, Carnarvon Basin, GSWA11193A, B, 1 internal mould of a dorsal valve

and 1 internal mould of a ventral valve from GSWA locality 44563, Glenburgh (1970) Run 9/047, pt. 322, EVG, BK8, Madeline Formation, Yard Grid 350-776, Carnarvon Basin.

DESCRIPTION: Specimens small and incomplete. Ventral valve internal moulds poorly preserved but indicate strong convexity and characteristic long, thin internal ridges. Rugae irregularly developed on ventral valves, not strongly raised. Dorsal valves possess pronounced, fine rugae, distinct, fine costellae and shallow, elongate dimples. Cardinal process minute and bilobed, median septum ill defined and short.

DISCUSSION: Although inadequate for detailed comparison this species is closest to *C. irwinensis* which species is distinguished by its distinct, fine rugae, regularly spaced, on the ventral valve.

AGE AND STRATIGRAPHIC RANGE: Coyrie and Madeline Formations, Carnarvon Basin. Early Baigendzinian (Middle Artinskian).

Cancrinella sp. B

Fig. 2S–V

MATERIAL AND LOCALITY: CPC19922A, B, 2 ventral valves from BMR locality ML51, Minilya River, north side, Minilya Syncline, 5 km west of Cundlego Well, *Cleiothyridina Strophalosia* horizon, early Kungurian, Norton (now Nalbia) Sandstone.

DESCRIPTION: Ventral valves strongly convex. Ears small and subquadrate. Rugae fine and low over visceral disc but coarse and prominent over pronounced trail. Ventral valve distinctly geniculated. Costellae relatively fine (2 per cm at 1 cm from the umbo), rounded and separated by narrow interspaces. Spine bases coarse (about the width of three costellae) and arise from swollen costellae. Body spines project at a low angle. Ear spines arranged in tuft formed by 2 rows of spines. Ventral umbo small pointed. Mature valve elongate with maximum width about mid length of valve.

Fig. 2—A–B, *Cancrinella bella* (Etheridge); from Noonkanbah Formation, Canning Basin. A–B, AMF16735, dorsal valve in ventral view, $\times 1.2$ and $\times 4.5$. C–O, *Cancrinella coolkilyaensis* sp. nov.; all from Coolkilya Greywacke, Carnarvon Basin. C–F, Holotype, CPC19920A, ventral valve internal mould in ventral, posterior and two lateral views, $\times 1.4$. G, CPC19920G, ventral valve external mould, $\times 1.2$. H–I, CPC19920B, ventral valve internal mould in postero-ventral and ventral views, $\times 1.5$. J, UWA88111, ventral valve internal mould in ventral view, $\times 1.2$. K, CPC19920E, incomplete internal mould of conjoined shell in dorsal view, $\times 1.5$. L, UWA88110, ventral valve internal mould in ventral view, $\times 1.5$. M–O, CPC19920F, external mould of dorsal valve in dorsal, interior and lateral views, $\times 1.4$. P–R, *Cancrinella* sp. A, P–Q, from Coyrie Formation, Carnarvon Basin; R, from Madeline Formation, Carnarvon Basin. P, CPC19921A, dorsal valve internal mould, $\times 1.6$. Q, CPC19921B, dorsal valve external mould, $\times 1.8$. R, GSWAF11093A, ventral valve internal mould, $\times 1.8$. S–V, *Cancrinella* sp. B; from Nalbia Sandstone, Carnarvon Basin. S–U, CPC19922A, ventral valve in posterior, ventral and lateral views, $\times 1.8$. V, CPC19922B, ventral valve in ventral view, $\times 1.8$.

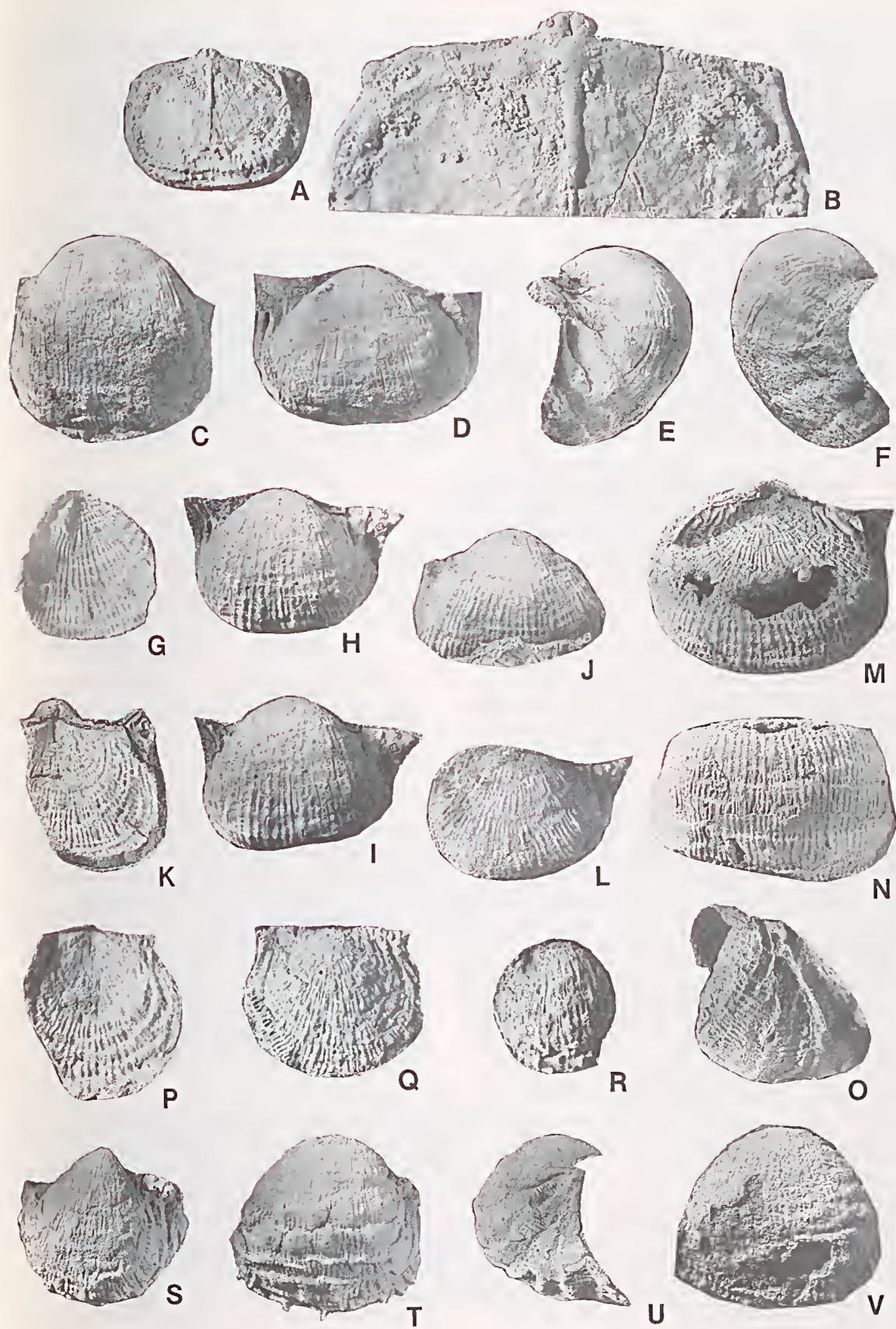


TABLE 3
MEASUREMENTS OF *Cancrinella* sp. B
e = estimate

Specimen number	Hinge width	Maximum width	Ventral length	Thickness
CPC19922A	14.0	17.0	18.2	12.5
CPC19922B	—	18.0	16.5	—

DISCUSSION: The highly convex ventral valve, coarse rugae on the trail and coarse spine bases indicate a distinct species. Spine bases and rugae are much coarser than those of *C. coolkilyaensis*. *C. bella* possesses relatively coarse spine bases but much more weakly developed rugae. The strongly developed rugae recall those of *C. magniplica* Campbell 1953 from the Kungurian of Queensland, but the east Australian species is much larger and somewhat less convex.

Genus *Lyonia* nov.

TYPE SPECIES: *Linoproductus cancriniformis* var. *lyoni* Prendergast 1943.

DIAGNOSIS: Moderately large, relatively gently concavo-convex linoproductinids, wider than long, maximum width at or close to hinge line. Hinge extremities flattened into large ears but not clearly demarcated from rest of valve. Ventral valve evenly convex—no flattening or sulcus, no distinct trail. Ventral ornament of fine rugae over entire valve, slightly stronger over ears and lateral flanks, distinct costellae, increasing in number normally by bifurcation, and spines. Spines as single row of curved hinge spines, smaller towards umbo and scattered body spines, in a generalised quincunx, arising from slightly swollen costellae. Ventral valve thin, internal ornament reflects external ornament, muscle scars vague even in largest specimens.

Dorsal valve thin, gently concave, weakly geniculate anteriorly; exterior ornament of fine rugae, distinct costellae, swollen elongate dimples and fine irregularly developed spines which are only developed after the initial 1.5 cm of growth of shell. Dorsal interior with fine median septum arising anteriorly of low, thickened pad which in turn is anterior of cardinal process. Cardinal process low and squat, not supported by septum, barely projects beyond hinge, weakly quadrilobed inferiorly, narrow and weakly bilobed exteriorly. Pair of low, broad ridges diverge from base of process; low marginal hinge ridges carry row of raised pustules (correspond to ventral hinge spines?). No brachial ridges; interior ornament reflects exterior ornament.

DISCUSSION: *Lyonia* is a distinctive monotypic genus. *Lyonia lyoni* is readily distinguished from *Linoproductus* by its external ornament, and from *Cancrinella* especially west Australian species, by its much larger size and more gentle ventral convexity (the latter is not an artefact of flattening or crushing). The presence of dorsal spines appears to be atypical of *Cancrinella* (see

Waterhouse & Gupta 1978). Nevertheless the dorsal interior of *L. lyoni* is quite distinct from that of *Cancrinella* where the cardinal process projects distinctly beyond the hinge line and is strongly supported by the median septum. The marginal hinge ridges of *Cancrinella* appear to lack the row of pustules that are present in *L. lyoni* (see Grigor'eva *et al.* 1977). The cardinal process of *Lyonia* recalls that of *Spitzbergenia* Kotlyar (in Grigor'eva *et al.* 1977), as shown in *S. gracilis* Kotlyar from the Late Permian Selandersk Suite of Spitzbergen, but Kotlyar's genus possesses stronger marginal ridges, a different median septum arrangement, weaker rugae over the shell and appears to lack dorsal spines. *Lyonia* may be ancestral to *Spitzbergenia*. *Auriculispina* Waterhouse 1975 from the early Permian of Queensland can be distinguished from *Lyonia* by its numerous ear spines, lack of dorsal spines and different dorsal median septum. *Bandoproductus* Jing & Sun (1981) is also close to *Lyonia* but lacks dorsal spines and has a higher cardinal process. The dorsal median septum of *Bandoproductus* is short and low when compared with that of *Lyonia*.

Lyonia lyoni (Prendergast 1943)

Fig. 3

1943 *Linoproductus cancriniformis* var. *lyoni*. Prendergast, p. 24, pl. 3, figs 1-2.

1957 *Linoproductus lyoni* Prendergast; Coleman (*partim.*), p. 76, pl. 8, figs 16-22.

HOLOTYPE: AMF36530, ventral valve, from 10 chains north west of Gnarrea Pool near Winning Station, Lyons Group, Carnarvon Basin.

MATERIAL AND LOCALITY: CPC19923A-F, 1 ventral valve, 1 ventral valve internal mould, 1 ventral valve external mould, 1 dorsal valve external mould and 2 dorsal valve internal moulds were measured. These and some 15 additional specimens of variable preservation are from BMR locality T23 (F17690 and F17692) approximately 4.8 km northeast of Round Hill Well, 210 m west of Kialawibri Creek road crossing, Winning Station, Carnarvon Basin, Lyons Group. Prendergast's (1943) syntypic series was re-examined.

Fig. 3—A-P, *Lyonia lyoni* (Prendergast); all from Lyons Group, Carnarvon Basin. A-B, CPC19923A, ventral valve in posterior and ventral views, $\times 1$. C, CPC19923F, internal mould of dorsal valve, $\times 1$. D, F-G, I-K, CPC19923D, internal mould of dorsal valve, $\times 1$, latex replica of dorsal valve internal mould in ventral view, $\times 1.2$, enlargements of mould of cardinal area, $\times 6$, and $\times 3.5$ respectively, enlargement of latex replica of cardinal region, $\times 4.5$. E, CPC19923C, incomplete external mould of ventral valve, $\times 1$. H, CPC19923B, ventral valve internal mould in ventral view, $\times 1$. J, L, CPC19923E, dorsal valve external mould, $\times 1$, enlargement of anterior of dorsal valve external mould, $\times 10$. M, AMF36530, rock slab with holotype (ventral valve in upper right) and dorsal valve internal mould, $\times 0.6$. N-O, AMF36530, holotype, ventral valve in ventral view, $\times 1$, enlargement of hinge spines, $\times 2$. P, AMF36530A, dorsal valve internal mould on slab of rock with holotype, $\times 1$.

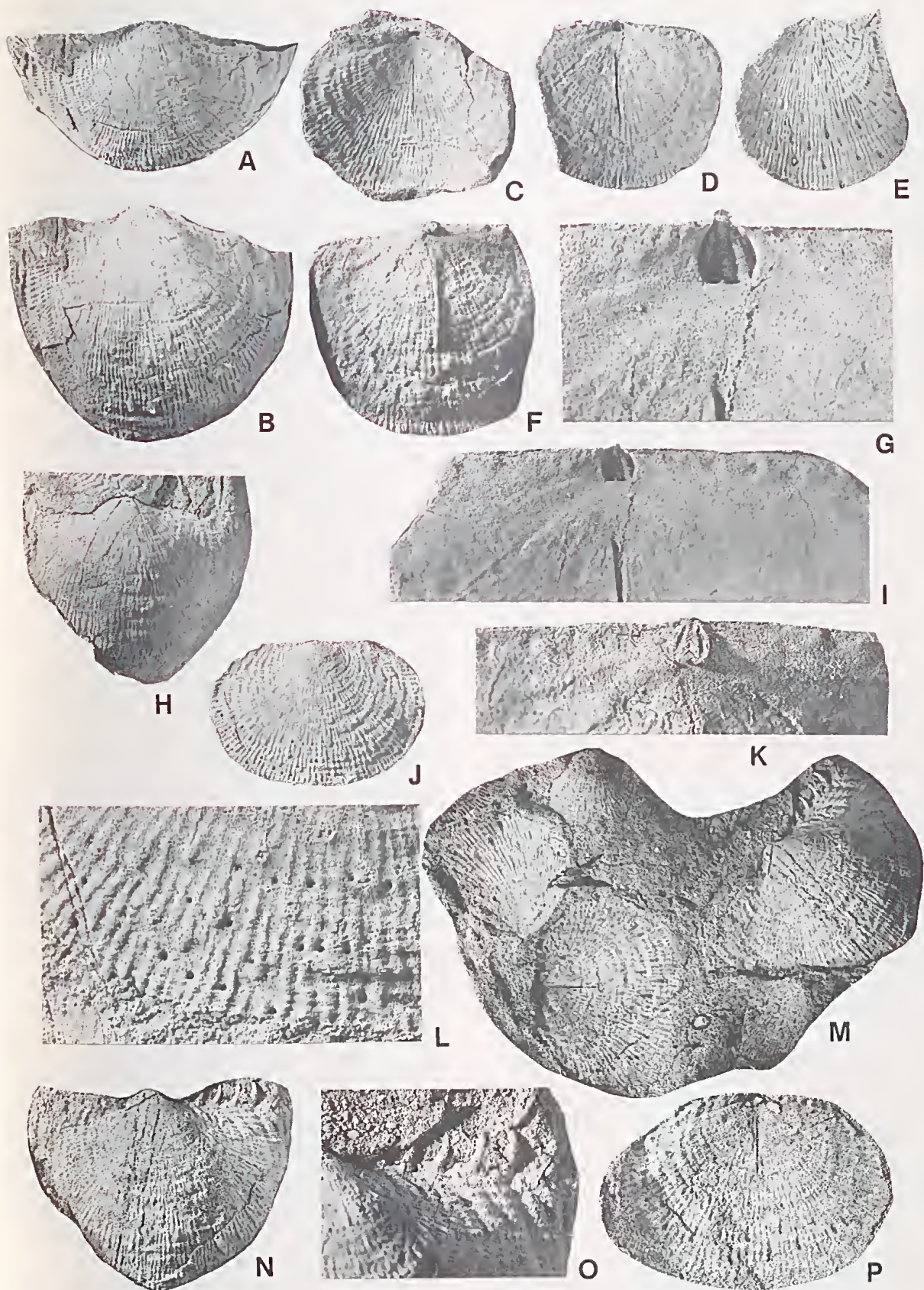


TABLE 4
MEASUREMENTS OF *Lyonia lyoni* (Prendergast 1943)
e = estimate; † = incomplete specimen

Specimen number	Maximum width	Hinge width	Ventral length	Dorsal length	Thickness	Dorsal septum length
CPC19923A	49.0e	49.0e	41.4	—	16.0e	—
CPC19923B	37.2e	36.5	27.5	—	12.5e	—
CPC19923C	—	—	26.0	—	—	—
CPC19923D	30.0e†	28.0e†	—	25.3	—	12.0
CPC19923E	29.8	—	—	22.0	—	—
CPC19923F	29.0	—	—	25.0	—	9.0

DIAGNOSIS: As for genus.

DESCRIPTION: Shell medium to large sized and transverse. Ventral valve evenly and moderately convex both transversely and in longitudinal profile; dorsal valve gently concave and weakly geniculated anteriorly (only by an increase of about 10° in concavity). Maximum shell width at or close to the hinge line. Ears large and flattened but not clearly demarcated from the rest of valves. No flattening or sulcus in ventral valve and no distinct ventral trail. Ventral valve with distinct ornament of relatively fine rugae over entire valve (about 10 per cm at 2 cm from umbo and about 6 per cm at 3.5 cm from umbo); rugae slightly stronger on ears and lateral flanks of valve. Costellae distinct (15 per cm at 2 cm from umbo and 10 per cm at 4 cm from umbo), rounded with narrow interspaces; cover entire ventral valve. Ventral spines of two types: a single row of curved hinge spines, smaller towards the umbo, and scattered, quincunxially arranged body spines over the remainder of the valve, growing from slightly swollen bases and arising from a single costella. Costellae invariably bifurcate anteriorly of spine bases and increase in number elsewhere on shell by bifurcation. Spines project forward at low angle to ventral valve. Ventral valve thin, internal ornament reflects the external ornament; muscle marks vague and ill defined even in largest specimens.

Dorsal valve thin, with external ornament of fine rugae, distinct costellae, swollen elongate dimples and fine, irregularly developed, erect spines, the latter only developed after initial 1.5 cm of growth. Dimensions of rugae and costellae similar to those for ventral valve. Body spines of ventral valve about 0.8 mm thick those of dorsal valve 0.3 mm thick. Dorsal interior with fine median septum arising anteriorly of low, thickened pad which, in turn, is anterior of low, squat cardinal process. Cardinal process not supported by septum, barely projects beyond hinge line; interior face of process with weakly divided, large median lobe and smaller lateral lobes giving a weakly quadrilobate appearance. Pair of low, broad ridges diverge from base of process and low, marginal hinge ridges carry row of raised pustules. No brachial ridges and interior ornament of valve reflects that of exterior.

DISCUSSION: Well-preserved dorsal valves are not known for species from New South Wales and Queensland that have been compared with *Lyonia lyoni* (Maxwell 1964,

Runnegar 1969, Degeling, & Runnegar 1979), but detailed comparison with true *Lyonia lyoni* is not possible until well preserved dorsal valves of the eastern Australian species are described and figured. The same is true for *L. lyoni* from the Tastubian of Afghanistan (Lapparent *et al.* 1971). *Cancrinelloides monticulus* Waterhouse (1982b) from the Asselian of southern Thailand, lacks dorsal spines and is distinct from *L. lyoni* in other ornamental details, such as density of ventral spine bases, as well as dorsal internal structures. It may be better assigned to *Bandoproductus*.

Coleman (1957) specimens (UWA32036, 32037a, 32037b) from the Callytharra Formation are re-assigned to *Cancrinella irwinensis*, a variable species, at times of large size.

AGE AND STRATIGRAPHIC RANGE: Lyons Group, Carnarvon Basin and Fossil Cliff Member, Perth Basin. Tastubian—possibly ranging to early Sterlitamakian.

Subfamily STEPANOVIELLINAE Waterhouse 1975

DIAGNOSIS: Linoproductinid shells with dominant costellate/capillate ornament and smooth, lobate ventral adductor scars at times dendritic anteriorly; small to medium-sized for family. Shell with subquadrate outline, ventral valve thickened.

GENERA INCLUDED AND DISCUSSION: The Stepanoviellinae, revised herein to include *Stepanoviella* Zavadovsky 1960, *Globiella* Muir-Wood & Cooper 1960 and *Liraria* Cooper & Grant 1975, is a distinctive group of linoproductids characterised by prominent fine radial ornament and by the possession of smooth, lobate, at times dendritic anteriorly, ventral adductor scars.

Waterhouse (1975) placed the Stepanoviellinae in the Anidanthidae. Recognition of the Anidanthidae has merit (Grigor'eva & Kotlyar 1977), but in view of the distinctive shape and ornament of the Stepanoviellinae, that subfamily is referred to the Linoproductidae. Waterhouse (1975, 1978a) stressed the nondendritic nature of the ventral adductors in his concept of the Stepanoviellinae. However, the nature of the ventral adductor scars should be used with caution in the classification of these productids. Waterhouse (1978a), while disputing the value of the genus *Pseudostrophalosia* Clarke (1970), stressed that dendritic ventral adductor scars develop late in ontogeny in the Strophalosiidae as in the Anidanthidae. *Yakovlevia* Fredericks (1925) possesses dendritic posterior adductor scars and lobate anterior adductor scars in the ventral valve. Grigor'eva *et al.* (1977) contrary to Muir-Wood and Cooper (1960) and Waterhouse (1970) have indicated that both *Stepanoviella* and *Globiella* possess elongate, dendritic adductor scars. Examination of specimens referred to *Globiella* from western Australia and India indicates that in old age the ventral anterior adductor scars of both species become weakly dendritic while the posterior adductor scars remain smooth.

Genus *Globiella* Muir-Wood & Cooper 1960

TYPE SPECIES: *Productus hemisphaerium* Kutorga 1844.

DIAGNOSIS: Medium sized shell, hemispherical, narrowing anteriorly producing elongate-oval outline in maturity; non-geniculate valves; ears small; umbo tiny; hinge width close to maximum width; both valves covered with fine radial costellae, at times flexuous anteriorly, bifurcating; dorsal valve with variably defined rugae; spines restricted to ventral valve, in row along hinge, increasing in size, rare or absent elsewhere on valve. Interior of ventral valve with weak ridges delimiting ears, smooth lobate to dendritic adductor scars and longitudinally striate diductor scars; dorsal interior with small, trilobate cardinal process; median septum on adult examples merged posteriorly into two fused ridges.

DISCUSSION: The above diagnosis is modified from those given by Muir-Wood and Cooper (1960) and Grigor'eva *et al.* (1977). Mature specimens of *Globiella foordi* possess poorly defined dendritic adductor scars and hence it is probably a feature that develops late in ontogeny. Grigor'eva *et al.* (1977) adopted a narrow diagnosis and range for the genus, but by enlarging the diagnosis, a large, widely distributed group of Gondwanan species can be included within *Globiella*. As noted by Fantini Sestini (1966) and Waterhouse (1970) the dorsal valve of many of these species is poorly known and hence assignment of various species to *Globiella* can only be provisional. Nevertheless, sufficient details of many of the species are known, to indicate that if they do not belong to *Globiella* they belong to a closely related (new) genus.

Grigor'eva *et al.* (1977) distinguished *Globiella* from *Stepanoviella*, the latter usually being treated as a senior synonym of *Globiella* (Grigor'eva 1962, Muir-Wood 1965, Waterhouse 1970). *Stepanoviella* Zavadovsky (1960), as restricted by Grigor'eva *et al.* (1977) carries two types of ventral spines—"inclined" and "straight"—as well as fine spines on the dorsal valve. *Stepanoviella* is characterised by extremely fine costellae and is reliably known only from the Late Permian of north-east Siberia.

Liraria Cooper & Grant (1975) is provisionally referred to the *Stepanoviellinae*. It is readily distinguished from *Globiella* by its transverse outline and poorly developed dorsal median septum, although otherwise the interior of the dorsal valves of both genera are somewhat similar (Cooper & Grant 1975).

Globiella umariensis (Reed 1928)

Fig. 4A-L

1928 *Productus umariensis* Reed. 371, pl. 31, figs 1-6; pl. 32, figs 4-8.

1928 *Productus umariensis* var *spinifera* Reed. 375, pl. 33, figs 1-6; pl. 35, fig. 9.

1928 *Productus rewahensis* Reed. 376, pl. 32, figs 1, 1a; pl. 35, figs 1-7.

1928 *Productus rewahensis* var *coroides* Reed. 378, pl. 32, figs 2-3a; pl. 35, figs 8-8a.

1965 *Globiella umariensis* (Reed), Mitra and Chakraborty. 91.

1977 *Stepanoviella umariensis* Sastry *et al.*, *Misc. Publ. Geol. Surv. India* 36: 94, pl. 1, fig. 5.

SYNTYPES: Series figured by Reed (1928, pl. 31, figs 1-6; pl. 32, figs 4-8).

MATERIAL AND LOCALITY: CPC19924A-M, 9 ventral valves, 3 ventral valve internal moulds (2 measured) and 1 incomplete dorsal valve all from Marine Bed (latest Tastubian), Narsarha railway cutting, Umaria, Madhya Pradesh, India; topotypes.

TABLE 5
MEASUREMENTS OF *Globiella umariensis* (Reed, 1928) in mm.
e = estimate; † = incomplete specimen

Specimen Number (all CPC)	Hinge width	Maximum width	Ventral length	Thickness	Length dorsal septum
19924A	32.0e	38.9	31.8	14.3e	—
19924B	29.2†	33.0†	26.8	12.8e	—
19924C	32.0e	34.0e	28.8	9.5e	—
19924D	29.5†	32.6	30.6	14.0e	—
19924E	28.0	28.0	23.0†	—	—
19924F	28.0†	33.0†	25.0†	—	—
19924G	27.0†	32.0†	—	—	—
19924H	—	—	28.5	—	—
19924I	26.4	37.0	—	—	—
19924J	16.5	21.4	16.5	—	—
19924K	—	36.0e	25.0†	—	—
19924L	—	16.0e	—	—	7.2

DIAGNOSIS: Large *Globiella*, transverse to elongate. Ventral valve with rugae on ears, at times on lateral flanks. Ventral spines, in row along hinge, variably developed over valve. Ventral valve convexity moderate for genus.

DESCRIPTION: Shell outline transverse from youth into maturity, becoming elongate in old age. Ventral valve with convexity increasing with old age; dorsal valve gently concave, not geniculated. Maximum shell width at hinge line from youth into maturity but moves to midlength of shell in old age. Ears small but distinct, clearly demarcated from rest of ventral valve by pronounced flattening. No flattening or sulcus in ventral valve and no demarcated ventral trail. Hinge line straight, carries row of ventral hinge spines, increasing in size away from small, pointed umbo. Spines variably developed over body of ventral valve, on some specimens extremely rare, other specimens carry spines at 5 mm intervals or closer. Body spines fine, arise from single costella, and project anteriorly at low angle to valve. Spine bases not swollen. Fine rugae developed on ears of ventral valve, variably developed on lateral flanks; they do not cross venter as distinct rugae but several specimens show 2-3 low wrinkles (best seen in oblique light) on anterior of venter. Costellae distinct, increase in number by intercalation and bifurcation, fine (10-11 per 5 mm at 1 cm from umbo and 8-9 per 5 mm at 2 cm from umbo), rounded and interspaces narrow. Ventral valve thin but external ornament not shown on

interior of valve. Muscle marks moderately clear; adductor scars posteriorly located and smooth in most specimens; specimen CPC19924M, an incomplete ventral valve internal mould, appears to possess striate or vaguely dendritic anterior adductor scars. Diductor scars large, broad and ridged with low branching ridges.

Dorsal valve thin, concave, with an external ornament of poorly developed, fine concentric wrinkles and distinct costellae, the latter being similar to those of ventral valve. Dorsal valve exterior appears to lack spines. Exterior ornament not reflected on interior of visceral disc despite shell being thin. Thin median septum extends from the base of cardinal process. Brachial ridges and cardinal process unknown but former not developed in one dorsal interior available to me.

DISCUSSION: Although originally described (Reed 1928) as two species and two varieties, this species was revised (Mitra & Chakraborty 1965) as one. I have examined two blocks from the type locality and concur with Mitra and Chakraborty (1965) on the variability of the species.

Details of the dorsal valve remain to be clarified—particularly the cardinal process and brachial ridges. Mitra and Chakraborty (1965, p. 92) indicated dorsal spines but Reed (1928) did not describe them and the fragmentary material available to me does not carry spines. I regard the species as lacking dorsal spines. Detached ventral spines of *G. umariensis* from the Umaria marine bed have been described and figured by Bhatia (1959) and Gupta (1971).

Many specimens of *G. umariensis* are of similar general outline to *L. lyoni* but the difference in internal ornament, spinosity (when it occurs in *G. umariensis*) and the dorsal septum indicate that the two species are not closely related. *G. umariensis* is assigned to *Globiella*, following Muir-Wood and Cooper (1960), rather than to *Stepanoviella* in the restricted sense (Grigor'eva *et al.* 1977). Nevertheless *G. umariensis* is an atypical species of the genus, frequently displaying a less globular and less convex appearance than typical *Globiella*.

The poorly known *G. gracilis* (Ching *et al.* 1977) is probably the closest species to *G. umariensis* as the Tibetan species also is only moderately convex ventrally and possesses similar constellae.

G. rossiae Fantini Sestini (1966) from the Early Permian (Aktastinian) of northern Iran is more sub-quadrate in outline and has finer costellae while the Aktastinian specimens and of the Pamirs (Grunt & Dmitriev 1973) is more strongly rugose than *G. umariensis*. The Pamir species is specifically distinct from *G. rossiae*. Other Early Permian species are discussed under *G. foordi* below.

G. umariensis has been recorded from the Early Permian of Afghanistan (Lapparent *et al.* 1971) but has not been fully described or figured. Specimens from the Early Permian of Afghanistan were compared by Termier and Termier (1971) with *Globiella flexuosa* (Waterhouse 1970b) by Termier and Termier (1971) who also provided a sketch of the dorsal interior with a long, thin median septum similar to that of *G. umariensis*.

Globiella foordi (Etheridge 1903)

Fig. 5

- 1890 *Productus tenuistriatus*: Foord (*non de Verneuil*). *Geol. Mag.*, Dec. III, 7: 151, pl. 7, figs 4, 4a.
- 1903 *Productus tenuistriatus* de Verneuil (?) var. *foordi* Etheridge, p. 19, pl. 1, figs 3, 4; pl. 5, fig. 22.
- 1907 *Productus tenuistriatus* var. *foordi* Etheridge fil. *Bull. geol. Surv. W. Aust.*, 27-30, pl. 9, figs 4-6.
- 1910 *Productus tenuistriatus* var. *foordi* Etheridge fil., Glaupert. *Bull. geol. Surv. W. Aust.*, 36: 37.
- 1931 *Productus tenuistriatus* var. *foordi* Etheridge fil., Hosking. *J. Roy. Soc. W. Aust.* 17: 8, 22.
- 1933 *Linoproductus* cf. *Linoproductus tenuistriatus* var. *foordi* (Etheridge, fil.), Hosking. *J. Roy. Soc. W. Aust.* 19: 47, pl. 4, fig. 3.
- 1937 *Linoproductus tenuistriatus* var. *foordi* (Etheridge fil.), Raggatt Fletcher. *Rec. Aust. Mus.* 20: 175.
- 1943 *Linoproductus cora* var. *foordi* (Etheridge), Prendergast, p. 22, pl. 3, figs 3-5.
- 1957 *Linoproductus cora* *foordi* (Etheridge), Coleman, p. 74, pl. 8, figs 10-15.
- 1971 *Stepanoviella foordi* (Etheridge), Waterhouse. *Proc. Pap. 2nd Gondwana Symp.*, p. 391.

LECTOTYPE: GSWAF156B selected by Crespin (1964, p. 68). Although stated to be the holotype by Crespin (1964), Etheridge (1903) did not select a type specimen. The specimen is from the Callytharra Formation at Fossil Hill, Wyndham River, Carnarvon Basin.

MATERIAL AND LOCALITIES: GSWA11193A-F, 6 ventral valves from Fossil Cliff, Irwin River, Fossil Cliff Member, Perth Basin; CPC19925, ventral valve internal mould from BMR locality 1R20, Carynginia Gully, 2.8 km on a bearing of 297° from Carynginia Well, Fossil Cliff Member; CPC19926A-C, 3 ventral valves from BMR locality GW87, Lat. 25°52', Long. 115°30', 10 to 17 m above base of Callytharra Formation, Carnarvon Basin; CPC19927A B, 2 ventral valves from BMR locality GW89, as for GW87, 17 to 21 m above

Fig. 4—A-N, *Globiella umariensis* (Reed), all from Umaria Marine Bed, India. A-B, CPC19924K, ventral valve in ventral and posterior views, $\times 1$. C, CPC19924D, ventral valve in ventral view, $\times 1$. D-E, CPC19924B, ventral valve internal mould in ventral and posterior views, $\times 1$. F, CPC19924J, ventral valve in ventral view, $\times 1$. G, CPC19924G, ventral valve in ventral view, $\times 1$. H, CPC19924L, dorsal valve interior, $\times 1$. I, CPC19924F, ventral valve in ventral view, $\times 1$. J-L, CPC19924E, ventral valve in anterior, ventral and lateral views, $\times 1$. M-N, CPC19924A, ventral valve in posterior and ventral views, $\times 1$. O-Z, AA-BB, *Globiella flexuosa* (Waterhouse), all from Jimba Jimba Calcarenite, Carnarvon Basin. O, MUGDF6030B, ventral valve in ventral view, $\times 1$. P-Q, MUGDF6030D, ventral valve in ventral and posterior views, $\times 1$. R-S, MUGDF6030I, ventral valve in ventral and posterior views, $\times 1$. T-U, MUGDF6030A, ventral valve in ventral and posterior views, $\times 1$. V-X, MUGDF6030C, ventral valve in ventral, postero-ventral and posterior views, $\times 1$. Y, MUGDF6030B, ventral valve in posterior view, $\times 1$. Z, AA, MUGDF6030F, ventral valve in ventral and posterior views. BB, MUGDF6030G, ventral valve in dorsal view, $\times 1$.



base of Callytharra Formation; CPC19928A, B, 2 natural casts of ventral valves from BMR locality G202, 9.2 km, bearing 335° from Lyons River Homestead, Callytharra formation; GSWA11194, a ventral valve from GSWA locality 44594, Yaringa (1968) Run 4/138, pt. 505 EVG BK9, Callytharra Formation, yard grid 343-726; GSWA11195, a ventral valve from GSWA locality 44559, Glenburgh (1970), yard grid 356,793, Photo Run 8/062, EVG BK8, pt. 277, Callytharra Formation; GSWA11196A-E, 4 ventral valves and 1 dorsal valve from GSWA locality 44573, Glenburgh (1970) Run 8/060, pt. 368, Callytharra Formation, type section, Callytharra Springs; MUGDF6029A-F, 6 ventral valves, from G. A. Thomas locality P498, type section, Callytharra Formation, Callytharra Springs, 34-38 m above base of formation. Sterlitamakian (Late Sakmarian).

TABLE 6

SIZE RANGES OF POPULATIONS OF *Globiella foordi* (Etheridge, 1903) in mm (including 2 gerontic Callytharra specimens).

Stratigraphic horizon	Hinge width	Maximum width	Ventral length	Thickness
Fossil Cliff	19.2-24.1	20.2-27.4	17.5-25.5	8.0-15.3
Callytharra	14.7-25.4	22.0-35.4	19.7-33.5	10.8-17.5
CPC19928A	—	40.0	45.0	26.0
CPC19928B	—	40.0	48.0†	30.0

DIAGNOSIS: Small to very large *Globiella*, transverse to elongate. Ventral valve normally without rugae, occasionally with several low rugae on ears and across venter. Ventral valve with row of hinge spines—no spines on remainder of valve. Ornament of distinct radial costellae, moderately coarse for genus. Dorsal valve with low rugae anteriorly.

DESCRIPTION: Shell outline transverse in youth and subquadrate to circular in maturity; gerontic shells elongate with distinct trail. Ventral valve strongly convex, globular in appearance, dorsal valve distinctly concave. Maximum shell width at hinge line from youth into maturity but moves to anterior of midlength of shell in old age. Ears small, pointed, normally poorly demarcated from body of ventral valve, at times twisted ventrally and hence prominent. No flattening of sulcus in ventral valve, the valve being evenly convex, except in gerontic specimens where convexity flattens out into pronounced trail. Trail in gerontic specimens medianly flat, strongly convex in transverse profile. Hinge line straight with row of ventral hinge spines, larger towards the ears and at low angle to hinge, point away from umbo. Ventral umbo small, pointed, overhangs hinge line. Spines absent over body of ventral valve. Rugae, developed weakly over small ears and posterior lateral flanks, low relatively fine and usually inconspicuous. Rarely, low undulations (or very weak rugae) cross venter of shell. Costellae distinct, increase in number by intercalation; normally straight but may curve and twist; secondary costellae may join primary costellae an-

teriorly and fuse into single costellae. Costellae normally curve and change orientation at sites of breakage during growth. Costellae sharply rounded and separated by distinct interspaces of about same width as costellae; size of costellae relatively constant (normally 16-18 per cm at 1 cm from umbo and 14-17 per cm at 2 cm from umbo) although a few specimens have finer costellae (e.g. MUGDF6029E, 22 per cm at 1 cm from umbo and 19 per cm at 2 cm from umbo). Ventral valve thin anteriorly, and appears to have been frequently broken during life, but thickened posteriorly along hinge and adjacent to muscle scars; trail particularly thin and normally missing. Muscle marks deep; adductor scars posteriorly located, elongate, lobate and smooth in juvenile specimens, in mature specimens they may be anteriorly ridged in feeble dendritic pattern. Diductor scars large, broad and feebly to strongly ridged and grooved with branching ridges.

Dorsal valve thin, delicate, moderately concave and has external ornament of poorly developed, fine, concentric wrinkles or rugae crossing visceral disc. Costellae distinct and increase by bifurcation; lower and, on available specimens, finer than those of typical ventral valve (19-20 per cm at 1 cm from the umbo). No dorsal spines. Ears distinct and twisted slightly ventrally. Exterior ornament reflected internally on anterior of visceral disc. Smooth adductor scars divided by sharp median septum and again bisected laterally by low ridges. Brachial ridges not developed on one available dorsal interior; cardinal process unknown.

DISCUSSION: The dorsal interior of *G. foordi* appears comparable with that of Sakmarian Afghan specimens compared with *G. flexuosa* by Termier and Termier (1971, fig. 9) although *G. foordi* appears to have a stronger median septum and wider adductor scars.

The remarkable feature of *G. foordi* is the distinctive trail in old age; the same type of trail is known in a gerontic specimen of *Globiella* (*Productus cora* Broili 1915, pl. 21, figs 4a-b) from Bitauini type faunas of Letti.

Fig. 5—A-Z, AA-GG, *Globiella foordi* (Etheridge); A-H, from Fossil Cliff Member, Perth Basin; I-Z, AA-GG, from Callytharra Formation, Carnarvon Basin. A-B, GSWAF11193B, ventral valve in ventral and posterior views, $\times 1$. C-E, GSWAF1193D, ventral valve in ventral posterior and lateral views, $\times 1$. F, GSWAF1193E, ventral valve in ventral view, $\times 1$. G-H, CPC19925, ventral valve internal mould in ventral and posterior views, $\times 1$. I-J, Q, CPC19926C, ventral valve in ventral, lateral and posterior views, $\times 1$. K-M, CPC19927A, ventral valve in dorsal, postero-dorsal, ventral and posterior views, $\times 1$. O-P, GSWAF11196A, ventral valve in ventral and anterior views, $\times 1$. R-T, GSWAF11196E, dorsal valve in dorsal, postero-ventral and ventral views, $\times 1.2$. U-V, MUGDF6029E, ventral valve in dorsal and ventral views, $\times 1$. W-X, GSWAF11196D, ventral valve in ventral and posterior views, $\times 1$. Y-Z, CPC19927B, ventral valve in ventral and posterior views, $\times 1$. AA, GSWAF11196B, ventral valve in ventral view, $\times 1$. BB, CPC19926A, ventral valve in ventral view, $\times 1$. CC, CPC19926B, incomplete shell in dorsal view, $\times 1$. DD, CPC19928B, natural cast of ventral valve in lateral view, $\times 1$. EE-GG, CPC19928A, natural cast of ventral valve in ventral, posterior and lateral views, $\times 1$.



That this form and the two large specimens from Western Australia are gerontic forms of *Globiella* appears inescapable as the costellae type and submature parts of the shells are typical of the species involved. The rarity of the gigantic individuals from Western Australia suggests that few specimens reached their maximum size potential and/or many large specimens were broken because the trail is extremely thin. A trail approaching that of *G. foordi* has also been figured for the Russian Kazanian species *G. hemisphaerium* (Nechaev 1911, pl. 1, figs 3b-c).

G. foordi is morphologically close to the younger *G. flexuosa* Waterhouse but can be distinguished by its smaller size at submaturity and its finer costellae. *Globiella* sp. from Bitauini, and correlated localities on the island of Timor (= *Productus cora* Broili 1916, pl. 1, figs 14, 15; pl. 2, figs 1-3; *Linoproductus cora* Shimizu 1966, pl. 16, figs 16-23) and also Letti, as discussed above, possesses costellae of similar strength to those of *G. foordi* (see Waterhouse 1970, p. 47) but can be distinguished from *G. foordi* by its clearly demarcated ears. *Globiella decempecta* (Lu 1982, pl. 1, figs 21-23) from the Artinskian Liangshan Formation of Sichuan Province, China is close to *G. foordi* with respect to its shell shape and ventral convexity. Costellae of the Chinese species are a little finer than those of *G. foordi*. *Linoproductus* cf. *foordi* (Yang & Ting 1962, pl. 24, fig. 5a, b) from the Early Permian of the Chi Lien Mountains, China, known from a single, moderately globular shell has fine costellae but its precise affinities are not clear.

G. umariensis is spinose and has costellae finer than those of *G. foordi*. *Globiella* sp. of Acharyya *et al.* (1975, pl. 2, fig. G) appears even more spinose than *G. umariensis*. The poorly known *G. gracilis* (Ching *et al.* 1977) also possesses fine costellae and appears to be less globular and ventrally convex than *G. foordi*.

G. rossiae (Fantini Sestini 1966) is less convex ventrally also has finer costellae than *G. foordi*. Kazanian *Globiella* from the Russian Platform and the Arctic possess costellae much finer than the Gondwanan species outlined above (Waterhouse 1970, Grigor'eva *et al.* 1977). They form a distinct, compact group of *Globiella* species that may well be generically distinct from Gondwanan species referred to the genus on details of ornament and trail.

Globiella flexuosa (Waterhouse 1970)

Fig. 40-Z, AA-BB

1970 *Stepanoviella flexuosa* Waterhouse, p. 45, pl. 14, figs 1-8, 15-16.

1971 *Stepanoviella flexuosa* Waterhouse. *Proc. Pap. 2nd Gondwana Symp.* p. 391.

HOLOTYPE: CPC8661 (Waterhouse 1970, pl. 14, fig. 2) an incomplete ventral valve from the Jimba Jimba Calcarenite, Carnarvon Basin.

MATERIAL AND LOCALITY: MUGDF6030A-N, 14 ventral valves from G. A. Thomas locality W758, type section of Jimba Jimba Calcarenite (Lat. 25°02.75'S, Long.

114°58.8'E) Jimba Jimba Station, 15 km west of Jimba Jimba Homestead. Aktastinian (Early Artinskian).

DIAGNOSIS: Medium sized *Globiella*, often transverse in outline. Ornament of distinct radial costellae, coarse for genus.

TABLE 7
MEASUREMENTS OF *Globiella flexuosa* (Waterhouse 1970)
in mm. e = estimate; † = incomplete specimen

Specimen number (all MUGD)	Hinge width	Maximum width	Ventral length	Thickness
6030A	26.5	33.0	—	14.0†
6030B	28.8	33.5	31.2	19.0e
6030C	29.0†	33.0	26.0†	—
6030D	—	31.0	28.5	15.0
6030E	—	29.0†	24.8	—
6030F	24.0	26.0	27.2	14.9
6030G	—	27.0†	25.4†	—
6030H	—	28.0	25.6	—

DESCRIPTION: Shell outline transverse to subquadrate and subcircular. Ventral valve strongly convex, globular. Maximum shell width at hinge line from youth into maturity but moves to about mid-length in old age. Umbo small, low, pointed and overhangs hinge line. Ears small, blunt and slightly twisted ventrally; poorly demarcated from remainder of valve. No distinct flattening or sulcus in ventral valve; valve evenly convex although some specimens are slightly less convex medially. No complete trail has been observed although one specimen, MUGDF6030B, indicates the presence of a trail. Hinge line straight, carries row of ventral hinge spines larger towards ears and at low angle to hinge and point away from umbo. Spines absent over body of ventral valve. Moderately distinct rugae developed over ears and lateral flanks of ventral valve and, at times, extend over visceral disc. Ventral ornament consists of radial, rounded costellae, increasing usually by intercalation; at times sinuous and increasing by bifurcation. Costellae, separated by wide interspaces, are relatively coarse (12-14 per cm at 1 cm from umbo and 10-12 per cm from umbo), the available collection suggesting that no specimens have costellae any finer. Ventral valve thin anteriorly but thickened posteriorly along hinge and adjacent to muscle scars. Muscle marks deep; adductor scars posteriorly located, elongate, lobate and smooth or anteriorly grooved. Diductor scars large, broadly oval and distinctly ridged and grooved.

Dorsal valve concave with small ears. Dorsal external ornament of fine concentric wrinkles or rugae crossing visceral disc and distinct costellae that increase by bifurcation. Costellae of comparable size to those of ventral valve judging from sole available specimen. No dorsal spines. Dorsal interior unknown.

DISCUSSION: The species is close to *G. foordi* but may be distinguished from Etheridge's species by its generally larger size at submaturity, often more pronounced ven-

tral rugae and consistently coarser costellae. The coarseness of the costellae of *G. flexuosa* sets the species apart from all other known species of the genus.

Specimens from the Early Permian of Afghanistan compared with *G. flexuosa* by Termier and Termier (1971) have not been fully described. *Stepanoviella flexuosa* of Jing and Sun (1981, p. 140, pl. 5, figs 7-8) from the Qinghai-Xizang Plateau possesses coarse costellae like the Western Australian species and although known from limited material, appears closely allied to *G. flexuosa*.

ACKNOWLEDGEMENTS

I thank Dr J. M. Dickins, Bureau of Mineral Resources, Dr A. E. Cockbain, Geological Survey of Western Australia, Mr D. Rhodes, University of Western Australia, Dr A. Ritchie, Australian Museum and Dr G. A. Thomas, University of Melbourne, for the loan of specimens. Dr G. A. Thomas read an earlier version of the paper. Isabel McDonald typed the manuscript and Linda Botham assisted with photography.

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LATE ORDOVICIAN GRAPTOLITES FROM THE MALLACOOTA BEDS, EAST GIPPSLAND

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ABSTRACT: Graptolite faunas have been discovered in slates near Mallacoota. Identifiable species suggest a late Gisbornian age for the Mallacoota beds in this region. The Mallacoota beds therefore accumulated prior to or as contemporaneous lateral facies equivalents of the undifferentiated Late Ordovician turbidite deposits that crop out in the same general region and as the Wagonga beds in southern N.S.W.

The sedimentary sequence cropping out between Eden (N.S.W.) and Mallacoota (Victoria) has been regarded as 'Undifferentiated Ordovician' and Steiner (1966) referred to it as the Mallacoota beds. Similar rocks occur westward (Fig. 1) along the coastal section to Orbost e.g., at Cape Everard (Douglas 1974, Fry & Wilson 1982). The assigning of an Ordovician age to these rocks was based on lithological similarities to sequences that underlie the fossiliferous Ordovician rocks elsewhere in East Gippsland (VandenBerg 1979a, b) and southern N.S.W., with the precise age remaining an enigma (Wilson *et al.* 1982). Graptolites have been reported from Cape Conran and Nowa Nowa with Hall (1899) recording that: 'from Eastern Gippsland, a few forms, also belonging to the Upper Ordovician, have

been doubtfully recorded, the condition of the specimens rendering specific identification impossible although I consider the generic character of the fossils sufficiently clear'.

However, Eaton (1980), during a study of the strongly foliated and metamorphosed sequence at Cape Conran, found no evidence for the existence of graptolites at this locality.

To date, only one graptolite locality has been identified in the Mallacoota beds. In April 1982 graptolites were found by P. de H. in a grey slate bed to the north of Seal Creek at 149°41'7"E, 37°39'16"S (Grid Reference 365278 Mallacoota, 1:100,000 Sheet 8822). At Cape Everard, where there is another portion of the Ordovician sequence, some conodonts have been collected

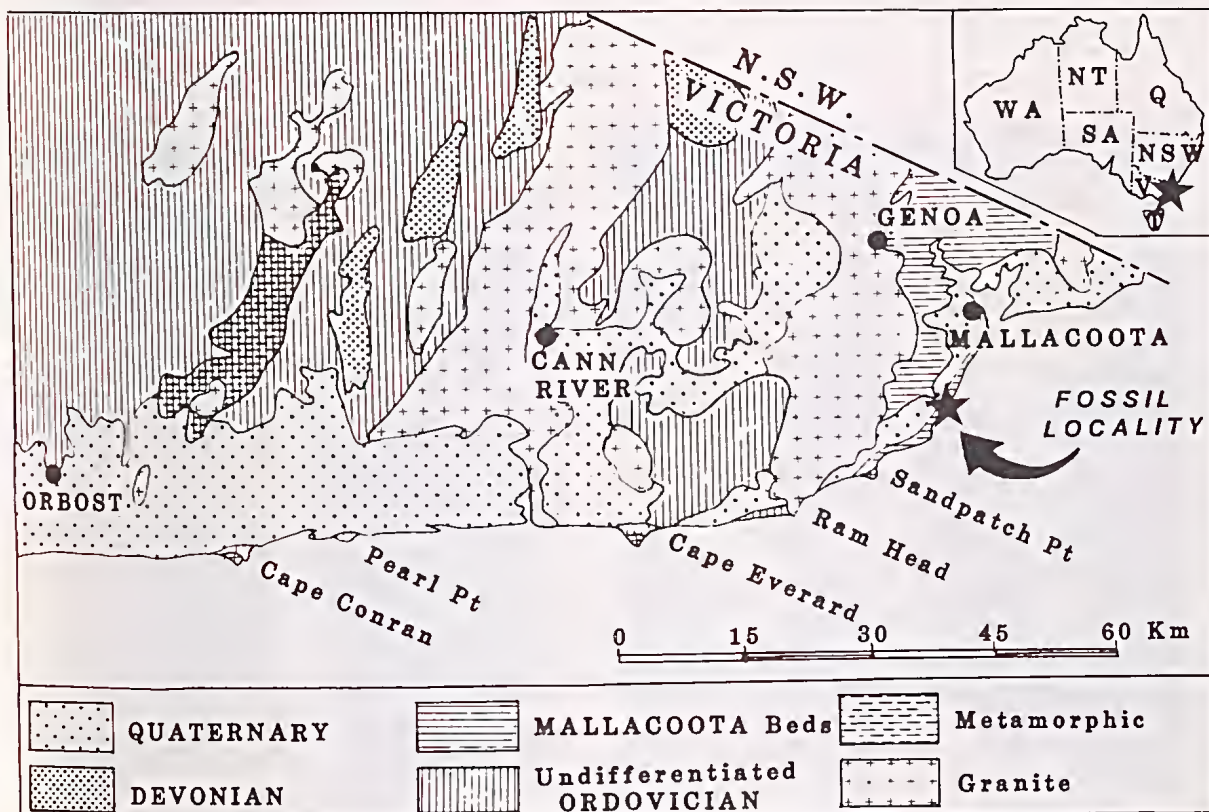


Fig. 1—Locality map adapted from Mallacoota 1:250 000 geological map (Douglas, 1974).

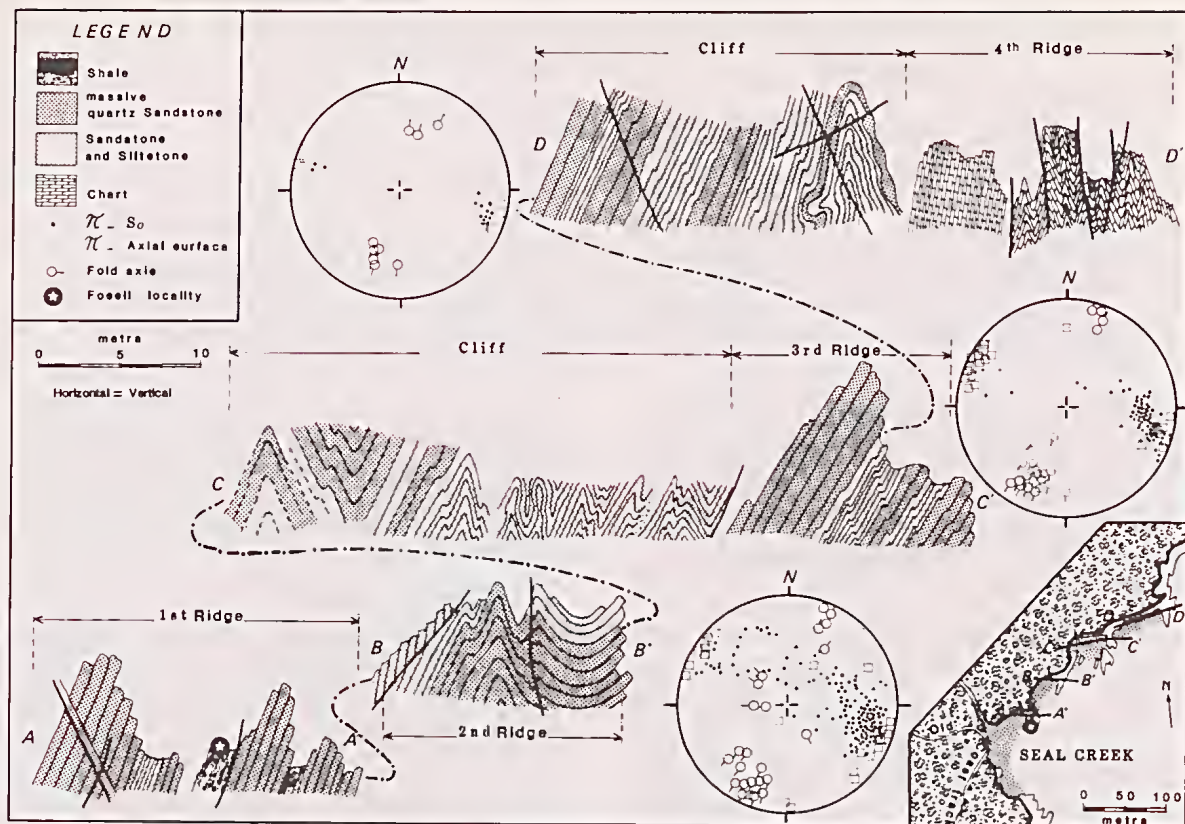


Fig. 2—Geological sections looking north showing the relationship of the graptolite locality to the sedimentary sequence and folding. The stereographic data are poles to bedding, axial surfaces of folds and fold axes, they are positioned adjacent to the section containing the data. Insert shows location of sections.

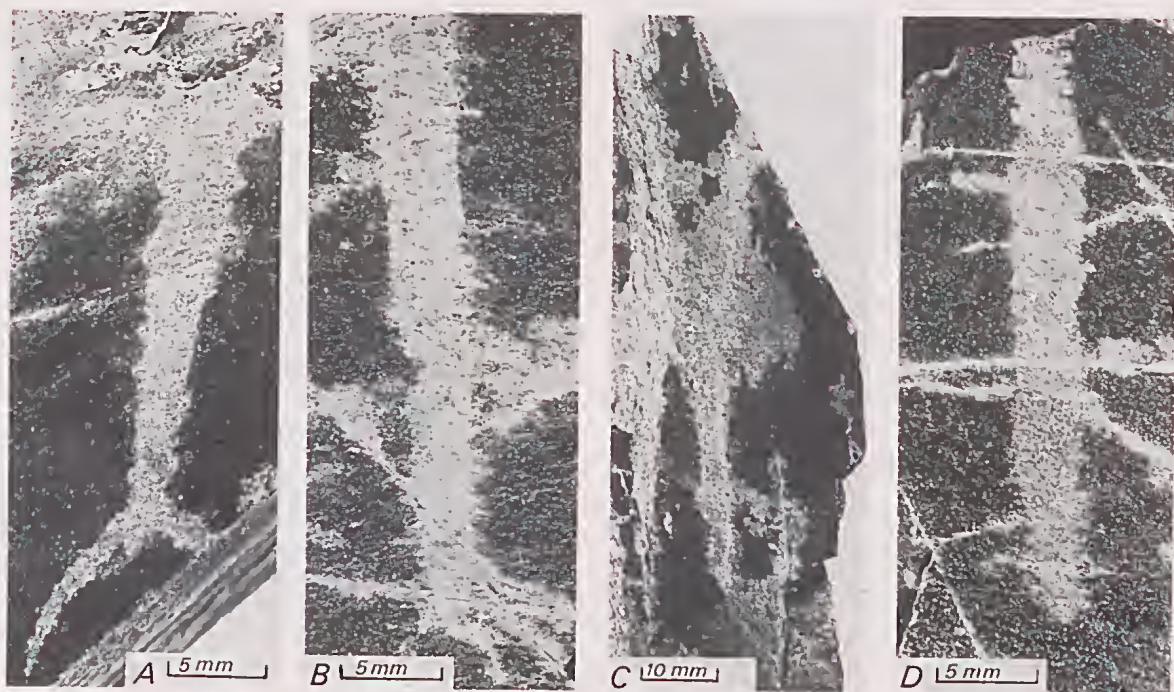


Fig. 3—Graptolites from Seal Creek, south of Mallacoota, Vic. A, B, *Climacograptus bicornis bicornis* (J. Hall). A, MUGDF6129b; B, MUGDF6139; C, *Dicranograptus ramosus* (s.l.) (J. Hall), MUGDF6148b; D, *Orthograptus calcaratus* (s.l.) Lapworth, MUGDF6145.

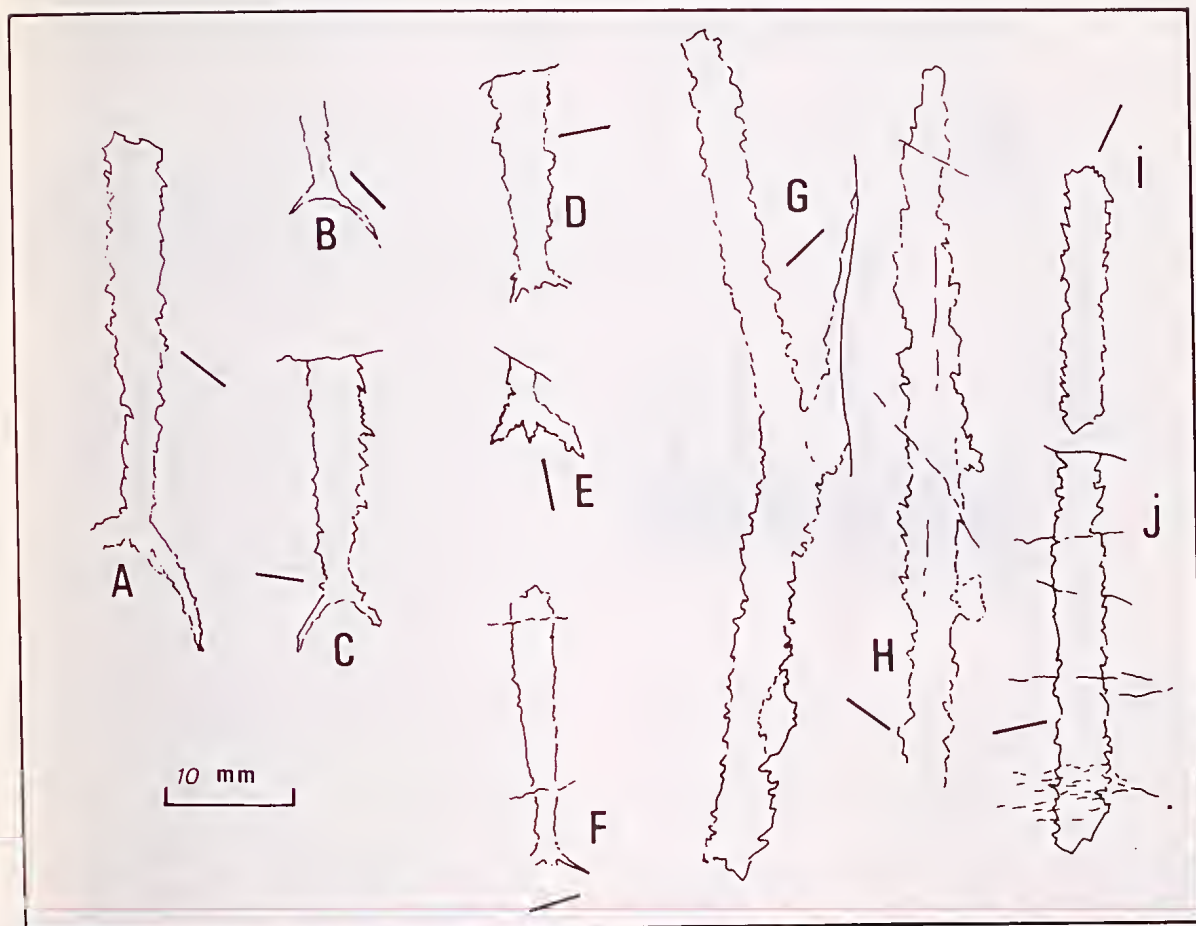


Fig. 4—Graptolites from Seal Creek, south of Mallacoota, Vic. A, B, C, *Climacograptus bicornis bicornis* (J. Hall). A, MUGDF6129a; B, MUGDF6133; C, MUGDF6143; D, E, F, *Climacograptus bicornis tridentatus* Lapworth, D, MUGDF6140; E, MUGDF6144a; F, MUGDF6141; G, H, *Dicranograptus ramosus* (J. Hall); G, MUGDF6148a; H, MUGDF6131a; I, J, *Orthograptus calcaratus* (s.l.) Lapworth, I, MUGDF6154; J, MUGDF6134. Lineation direction on samples shown by short lines.

and identified by I. Stewart (pers. comm. and see VandenBerg 1981); these suggest a Late Ordovician age.

GEOLOGICAL SETTING

The sequence containing the graptolite horizon is illustrated in Fig. 2 and consists of folded sandstones, shales and cherts. It is similar to that described 10 km to the north by Fenton *et al.* (1982), being characterised by turbidites deposited in the mid-fan region of a submarine fan. Three main episodes of deformation accompanied by lower greenschist facies metamorphism have affected the sequence. The structure at Seal Creek (Fig. 2) is dominated by upright folds with subvertical axial surfaces, the majority of the fold axes plunge 20° towards the SSW. In this area there is a slaty cleavage which subparallels bedding. The graptolite locality (Section A-A') lies on the limb of a major asymmetric fold which folds the earliest cleavage and bedding. The graptolites occur in an 80 cm length of a grey shale bed (20 cm thick). The rest of the bed is disturbed by joints, faults and quartz fillings and has yielded no fossils.

THE GRAPTOLITE FAUNA

Approximately 80 graptolite impressions have been found as white phyllosilicate or silvery carbonised films. The state of preservation is generally poor with the graptolites being smeared out and the thecal forms are often not apparent. Two biostratigraphically important species have been identified, namely: *Climacograptus bicornis bicornis* (J. Hall) (Fig. 3A, B, 4A-C) and *Dicranograptus ramosus* (J. Hall) (Fig. 3C, 4G, H). Two other poorly preserved species have been identified: these are *Climacograptus bicornis tridentatus* Lapworth and on the basis of the thecal shape *Orthograptus calcaratus* (subspecies could not be determined).

Three of the identifiable forms are confined to the Late Ordovician (Fig. 5) and have been determined as Gisbornian [Gi(m) or Gi(u)] by reference to the published ranges of VandenBerg (1981) and Thomas (1960). A lower limit for the age is given by the appearance of *C. bicornis bicornis* and *D. ramosus* (Fig. 5). A more restricted age is given by the presence of *C. bicornis tridentatus* and *O. calcaratus*. Therefore an upper age

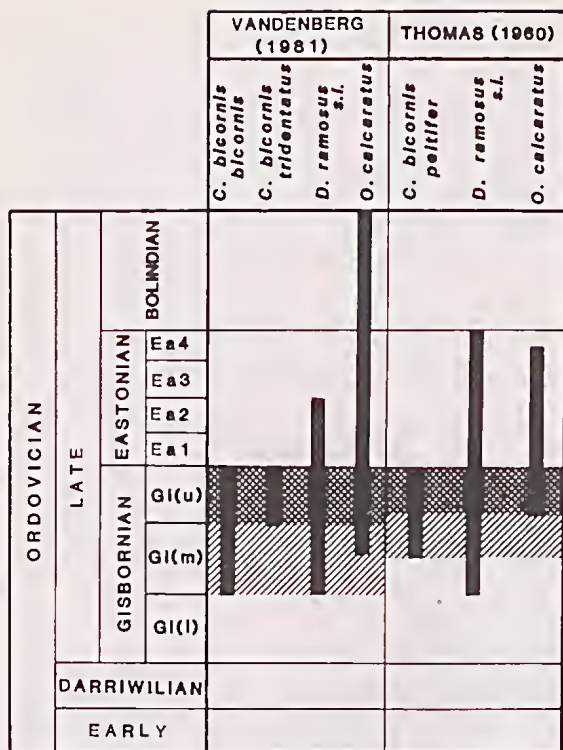


Fig. 5—Age range of graptolites identified at Mallacoota.

for the sequence is the Gisbornian-Eastonian boundary, suggested by the disappearance of *C. bicornis bicornis* and *C. bicornis tridentatus*.

The fossils MUGDF6126a to F6188 are lodged in the F. A. Singleton Museum, Geology Department, University of Melbourne.

CONCLUSIONS

The graptolite faunas suggest that deposition of this part of the Mallacoota beds was during the Gisbornian division of the Late Ordovician, only just older than the Eastonian units in other parts of East Gippsland (VandenBerg 1979a, 1979b, 1981). The deposition of the Mallacoota beds in northeastern Victoria may be con-

temporaneous with parts of the Wagonga beds and other slate and greywacke units in N.S.W. (Jenkins *et al.* 1982).

ACKNOWLEDGEMENTS

We wish to thank the National Parks Service for permission to work in the Croajingalong National Park. We thank N. W. Archbold for his help with specimen photography and O. P. Singleton and A. H. M. VandenBerg for their help in identifying the graptolites.

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PALAEOZOIC GEOLOGY OF THE DARTMOUTH DAM AREA, NORTHEASTERN VICTORIA

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ABSTRACT: The arcuate Wombat Creek Graben in the Dartmouth area of Northeastern Victoria is bounded on the east and west by Ordovician metasediments and localised areas of higher grade regional metamorphics and associated granitic rocks of the Omeo Metamorphic Complex. Acid to intermediate volcanic sequences, which are largely confined to the graben, were originally all included in the Mitta Mitta Volcanics but are now subdivided. The Silurian Mitta Mitta Volcanics consisting of dacite to rhyodacite are restricted to the southern part of the graben. In the north, a complex unit of dacite to rhyolite, named the Dartella Volcanic Group, is of possible Early Devonian age. Late Silurian clastic sediments comprising the Wombat Creek Group occur in the southern part of the graben. A number of Silurian to Devonian intrusives, some of which were intruded along faulted margins of the graben, range from quartz-diorite to muscovite granite. The volcanics of the Dartella Volcanic Group may be genetically related to some of these intrusions.

Filling of the reservoir of the Dartmouth Dam commenced in 1977 and much of the geological exposure in the Mitta Mitta River Valley upstream of the dam site has been lost to future workers. This paper is a summary of data collected during geological mapping by the authors between 1974 and 1978 and is intended to be an introductory description of the Palaeozoic geology of the flooded area and some of the surrounding district. It expands on regional mapping and detailed site investigations undertaken during construction of the Dartmouth Dam (S.R.W.S.C. 1980).

The area lies in the Eastern Highlands approximately 300 km northeast of Melbourne and is located to the east of the main Omeo Metamorphic Complex (Fig. 1). It is a zone of structural complexity which underwent intermittent igneous activity during the Silurian and the Devonian (VandenBerg 1978). Upper Cainozoic basalts and fluvial deposits occur within the area but are not described in this report. Rock samples collected are lodged at Monash University, the University of Sydney and with the Geological Survey of Victoria.

STRATIGRAPHY

ORDOVICIAN METASEDIMENTS

Pre-metamorphic Pile

Low grade metasediments form the bedrock surrounding the igneous and higher grade metamorphic complex at Dartmouth and the Wombat Creek Graben (VandenBerg *et al.* in press). The nature of the premetamorphic succession can only be determined by examination of low grade chlorite-quartz-white-mica (rarely biotite-bearing) slates, metasiltstones and meta-quartzites. Even at low metamorphic grade, recrystallisation is well advanced and adjacent to large intrusions, medium and high grade schistose and hornfelsic metamorphic aureoles occur.

The Ordovician succession consists of an undetermined thickness of well bedded quartz-rich sandstone, siltstone, shale and thin rare cherts and siliceous limey beds. No basic igneous rocks of this age occur in the study area. Thick sandy beds are turbidites (Bolger 1982) displaying upward grading from coarse sandstone and siltstone to fine shaly layers having planar lamination, ripple drift cross-lamination and ripple marks. Load casts and flame structures are commonly developed. Sandstones are usually quartz-rich greywackes, with locally abundant detrital feldspar. Muscovite, tourmaline and zircon are also common detrital components. Shales are often laminated and discrete black shale (slate) units up to 30 m thick occasionally contain poorly preserved graptolites. The low-grade metasediments grade westwards into higher grade regional metamorphics in the Omeo Metamorphic Complex. Medium and high grade metamorphics also occur in the Dartmouth area.

Age

There are a number of widely spaced graptolite localities in low grade metasediments in the Dartmouth area. All contain Late Ordovician (usually Eastonian but occasionally Gisbornian or Bolindian) forms (Bolger 1978). In medium grade schists in the Eskdale area, early Bendigonian graptolites have been recovered (Kilpatrick & Fleming 1980). However, the relative scarcity of graptolite localities and the lack of marker horizons in this multi-deformed sequence, precludes definition of a regional younging direction.

Medium and High Grade Ordovician Metasediments

Along both the Dartmouth-Mt. Benambra Road and the Yankee Point Track, low-grade Ordovician metasediments grade into knotted phyllites, quartzites and schists. To the west of Mitta Mitta Township, they grade

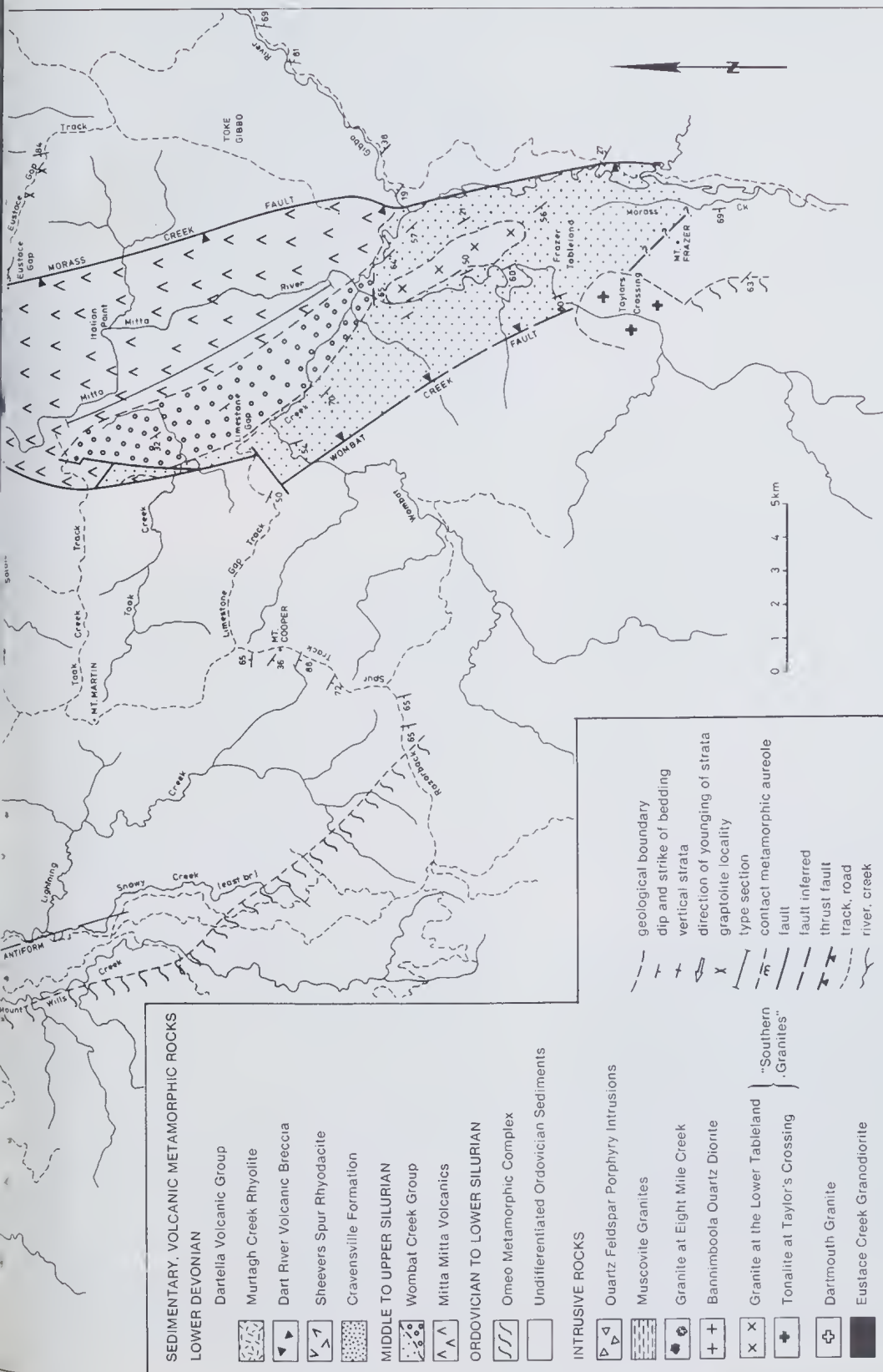


Fig. 1—Geological Map of the Dartmouth Dam Area.

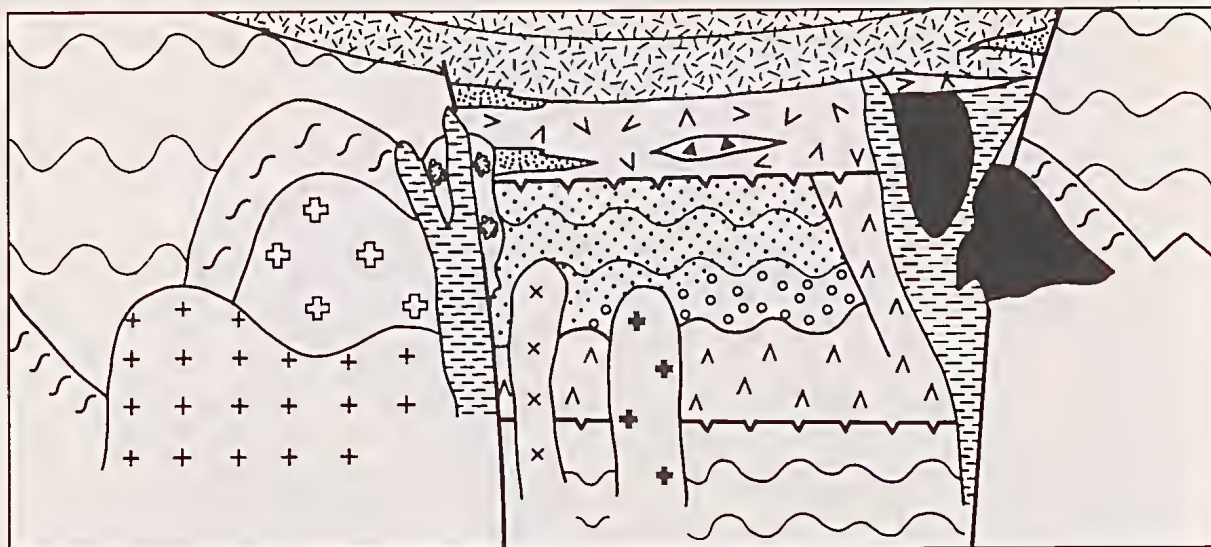


Fig. 2—Rock relation diagram for the Wombat Creek Graben. (Symbols as for Fig. 1).

into phyllites and schists of the Omeo Metamorphic Complex. The increase in metamorphic grade is marked by the appearance and increase in grain size of cordierite and/or andalusite porphyroblasts. In road cuttings along the Dartmouth-Mt. Benambra Road, the lowest grade rocks are knotted phyllites comprising pinitized cordierite porphyroblasts up to 1.5 cm long within a strongly foliated quartz-muscovite-biotite matrix. At higher metamorphic grade approaching the Dartmouth Granite boundary, crenulated muscovite-biotite-quartz knotted schists with large cordierite and/or andalusite porphyroblasts grade into higher grade sillimanite-bearing banded schists and gneisses adjacent to the granite. On the Yankee Point Track, knotted phyllites with coarse cordierite and/or andalusite porphyroblasts, grade into quartzite and biotite schist near the contact with the Eustace Creek Granodiorite.

SILURIAN

Mitta Mitta Volcanics

A linear belt of dacite, rhyodacite, rhyolite and volcanic breccia extends from the junction of the Gibbo and Mitta Mitta Rivers as far north as Cravensville. This suite was collectively named the Mitta Mitta Volcanics by Talent (1959) and was later referred to by Talent (1965), Singleton (1965) and Talent *et al.* (1975). They were mapped but not differentiated by Bolger and King (1976). Subsequent mapping and petrographic examination has shown that the rocks in this belt comprise three volcanic and one partly sedimentary unit representing at least two different volcanic episodes within the area. The Mitta Mitta Volcanics are here restricted to the southernmost suite of dacite and rhyodacite which outcrops from south of Yankee Point to the confluence of the Mitta Mitta and Gibbo Rivers (Bolger 1982). The volcanic rocks north of Yankee Point towards Mount

Cravensville are herein called the Dartella Volcanic Group.

The best exposures of Mitta Mitta Volcanics were along the Mitta Mitta River. The following discussion of the unit is based on observations made in the section along the river which would have been the logical type section had it not been inundated. The only other accessible area of exposure is along the main ridge south of Eustace Gap between the Mitta Mitta River and the Toke Gibbo Track and this is proposed as a type area for the Mitta Mitta Volcanics (Bolger 1982) (between G.R. 555388 and 588327 Benambra 1:100 000 topographic map). Outcrops of the Mitta Mitta Volcanics are massive, forming steep bluffs overlooking the Gibbo River and large rapids on the Mitta Mitta River. Apart from a thin tuff band and occasional columnar jointed units (Fig. 3), the Mitta Mitta Volcanics are mesoscopically structureless. In outcrop, the rocks are generally green-grey, purple-brown and white with sparse fine grained phenocrysts. At the Mitta Mitta-Gibbo River junction, near the contact with the Wombat Creek Group, there are occasional pyrite cubes. The rocks contain bipyramidal embayed quartz phenocrysts, prismatic and zoned plagioclase, rare potash-feldspar and some altered biotite (Fig. 4). Xenoliths are rare to absent. The groundmass is highly chloritic. Primary ignimbritic textures were recognised in only one sample which contained undistorted, devitrified glass shards. Spherulites are abundant, perlitic cracks are common (I. A. Nicholls *pers. comm.* 1979) and there are occasional cavities lined with chalcedonic silica.

Brecciated volcanics (? flow breccias) consisting of clasts of acid volcanics up to 20 cm diameter in a fine grained green chloritic matrix outcrop along the Mitta Mitta River at a number of localities.

The Mitta Mitta Volcanics are considered to post-date the Ordovician beds and are faulted against them



Fig. 3—Columnar joints in southerly dipping Mitta Mitta Volcanics, Mitta Mitta River, 1 km north of Gibbo River junction.

Volcanics are overlain by the Upper Silurian Wombat Creek Group which contains acid volcanic detritus derived from the Mitta Mitta Volcanics in its basal conglomerate (Singleton 1965, Bolger 1982). The Mitta Mitta Volcanics are therefore post-Late Ordovician in age and may be as young as Wenlockian (Middle Silurian). They are possibly time equivalents of the Douro Group of the Yass area in New South Wales (Pogson & Baker 1974) and are probably equivalent to the Thorkidaan Volcanic Group east of Benambra (VandenBerg *et al.* in press).

Wombat Creek Group

The Wombat Creek Group is exposed from Toaks Creek southward to near Taylors Crossing. The best exposures were in the river sections now inundated by the reservoir. There is a small outlier in the Benambra area along Morass Creek. The Wombat Creek Group is in excess of 3800 m thick and consists of three formations—the Toaks Creek Conglomerate, the Gibbo River Siltstone and the Tongaro Sandstone, which have been described in detail and discussed elsewhere (Bolger 1982).

The Toaks Creek Conglomerate consists of massive grain-supported conglomerate containing well rounded clasts up to 35 cm in diameter, underlain by a thin basal unit of green-grey siltstone, feldspathic sandstone and pebbly sandstone. Clasts consist of quartzite and quartzitic sandstone, chert, acid volcanics derived from the underlying Mitta Mitta Volcanics, siltstone, minor granite and reef quartz. Towards the top of the Conglomerate along the Mitta Mitta River, recrystallised limestone clasts occur.

The Toaks Creek Conglomerate is overlain by the Gibbo River Siltstone consisting of bioturbated

fossiliferous brown and green siltstone with interbedded quartz sandstone, conglomerate and lenticular limestones near the base. The conglomerates contain quartzite and granitic clasts. Shelly fossils in the siltstones and limestones include corals and brachiopods which indicate a Late Silurian (Ludlow) age (Talent 1959, 1965, Talent *et al.* 1975).

The uppermost unit of the Wombat Creek Group, the Tongaro Sandstone, consists of well-bedded fine to medium grained turbiditic quartz sandstone and interbedded black siltstone. In the southern part of the belt, there are interbedded limestones which contain shelly fossils (Talent 1959, 1965, Talent *et al.* 1975) and conodonts (Cooper 1977), suggesting a Late Silurian age. In the northwest near Wombat Creek, the Tongaro Sandstone contains massive conglomerates consisting entirely of well-rounded quartzite clasts. The top of the sequence is faulted against the Ordovician by the Wombat Creek Fault which is exposed along the Limestone Gap Track. The Wombat Creek Group overlies the Mitta Mitta Volcanics, although structural complexity at the contact has masked stratigraphic relationships between the two units. Along the Mitta Mitta River, the volcanics dip southwesterly beneath the Wombat Creek Group, except in a highly complex zone at the contact. In this zone, the sequence is overturned so the volcanics appear to overlie sediments which are faulted, folded, overturned and have a pronounced fracture cleavage. Along the Gibbo River, the volcanics have been thrust over the Wombat Creek Group giving the false appearance of an unconformity, with the volcanics appearing to post-date the sediments.

DEVONIAN

Dartella Volcanic Group (Named after the Parish of Dartella)

Introduction: The Dartella Volcanic Group is a new name introduced to include an intermediate to acid volcanic suite extending from Yankee Point to the

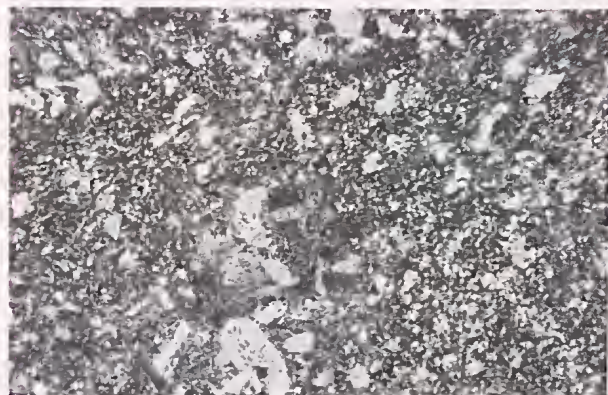


Fig. 4—Photomicrograph of altered dacite showing fine grained spherulitic groundmass, Mitta Mitta Volcanics. Aggregate at top centre consists of plagioclase, chlorite and minor epidote. ($\times 30$)



Fig. 5—Eutaxitic texture in rhyodacitic lapilli tuff, Sheevers Spur Rhyodacite, Mitta Mitta River near Larsen Creek Junction.

Lightwood area, north-east of Cravensville. The Group comprises the Cravensville Formation, Sheevers Spur Rhyodacite and the Murtagh Creek Rhyolite. These units were originally included in the Early Silurian Mitta Mitta Volcanics (Talent 1959, 1965, Talent *et al.* 1975, Singleton 1965, Bolger & King 1976, Bolger & Rogerson 1978a) but on structural and petrographic grounds, are now considered to be a separate Group, possibly of Early Devonian age. The volcanics of the Dartella Volcanic Group are petrographically distinct from the Mitta Mitta Volcanics and are much less altered.

Cravensville Formation (Named after Mount Cravensville): The Cravensville Formation is a sequence of interbedded black siltstone, tuffaceous sandstone and breccia and thin ignimbritic units. It is best exposed on a spur trending west from Mount Benambra (between G.R. 505592 and 492595, Benambra 1:100 000) and this is designated as the type section. Small outcrops of slate breccia, volcanics, quartzites and slate referred to the Cravensville Formation occur on the spur between Green and Larsen Creeks, the Sassafras Gap Track, the Dart River and the Yankee Point Track. A small exposure of gently dipping sediments near Shady Creek is tentatively included in the Cravensville Formation.

Sedimentary breccias are characteristic of the Cravensville Formation, consist of tightly packed, angular slate clasts up to 5 cm in diameter, and are often silicified. Sandstones (quartzites) contain abundant metamorphic quartz, plagioclase, alkali feldspar, tourmaline and brown hornblende. Interbedded volcanic units are thin and perhaps in places reworked, although along the spur between Greens and Larsen Creeks, eutaxitic texture typical of the Sheevers Spur Rhyodacite occurs. Black siltstones and tuffaceous sandstones often have a poorly developed cleavage. The Cravensville Formation is always exposed at or near the margins of the volcanic units. It is considered to represent material accumulated at the margins of the Graben prior to or during major volcanic episodes. It is associated with volcanic units from the top to the bottom of the Dartella Volcanic Group and is thus considered to be diachron-

ous. The steep dips and cleavage in parts of the Cravensville Formation, compared with the relatively gentle dips of the volcanic units, are attributed to movement on nearby faults and the more ductile response to deformation of the sedimentary rocks.

Sheevers Spur Rhyodacite (Named after Sheevers Spur, Mitta Mitta River): Ignimbritic rhyodacite and dacite with subordinate andesite and rhyolite form the southernmost unit of the Dartella Volcanic Group and are collectively named the Sheevers Spur Rhyodacite. As with the Mitta Mitta Volcanics, the best exposures were along the Mitta Mitta River but are now inundated. The designated type area is west of the Mitta Mitta River along the Sheevers Spur Track between G.R. 517503 and 513453.

The unit is variable in composition, grain size and xenolith composition. Eutaxitic texture (Fig. 5) is well developed in welded volcanoclastics demonstrating that the Sheevers Spur Rhyodacite is ignimbritic. Rocks of this suite contain up to 20% phenocrysts and varying amounts of flattened pumice or clastic fragments. They are distinguished from the Mitta Mitta Volcanics and the Murtagh Creek Rhyolite by the abundance of pyroxene phenocrysts and igneous rock fragments.

Feldspars are the most abundant phenocrysts and are always altered. Plagioclase is mostly andesine in the rhyodacites but as calcic as labradorite in the dacites. Some plagioclase is zoned with extensively altered cores. Alkali-feldspar, when present, is greatly subordinate to plagioclase. Quartz occupies only 3 to 5% of the rocks and is typically found as embayed, cracked hexagonal grains. Chloritised (?) pyroxenes are ubiquitous and occur as prismatic blocky grains. Biotite is present but not common. Inclusions of slate, sandstone and flattened pumice are common to abundant. Granitic and acid volcanic clasts of variable size and abundance are ubiquitous. The groundmass is fine grained, quartzofeldspathic and highly chloritic. Spherulites are present. No cuspat, undevitrified glass shards are preserved but there is a pronounced banding around phenocrysts and clasts, suggesting original eutaxitic layering.



Fig. 6—Concentration of granitic, and subordinate volcanic and sedimentary clasts in fine grained groundmass; Dart River Volcanic Breccia, Dart River.

In the Dart River area, dacitic to andesitic rocks containing large, often twinned augite phenocrysts in a very fine grained quartzo-feldspathic groundmass and a minor occurrence of rhyolite with abundant quartz in a devitrified groundmass are included in the Sheevers Spur Rhyodacite.

Within the Sheevers Spur Rhyodacite, outcropping in the Dart River between G.R. 625538 and 552549 is a complex unit here named the Dart River Volcanic Breccia containing lithic clasts usually up to 30 cm in diameter but some up to 1 m. Clasts are mainly igneous (Fig. 6) and consist of Sheevers Spur Rhyodacite and granite, as well as sandstone, slate and rare pegmatite. It has a fine-grained quartzo-feldspathic groundmass. The Dart River Volcanic Breccia passes into a rhyolite of the Sheevers Spur Rhyodacite on the northern side of the Dart River and is gradational with rhyodacites, dacites and andesites to the south and west. Its stratigraphic position within the Sheevers Spur Rhyodacite is not clear.

Murtagh Creek Rhyolite (Named after Murtagh Creek): A unit of ignimbritic rhyolite, rhyodacite and agglomerate outcrops on the Mount Benambra-Dartmouth Road and extends as far north as the Lightwood Track, north-east of Cravensville. It is here named the Murtagh Creek Rhyolite and the type section is the section exposed along the Dartmouth-Mount Benambra Road (G.R. 500560 and 513596). The rocks are often deeply weathered although locally they form steep bluffs and high peaks such as Mounts Benambra and Cravensville. A massive siltstone is exposed at the base of the sequence near Tallangatta Creek. When fresh, the Murtagh Creek Rhyolite is generally strongly welded, dense, grey to grey black in colour with euhedral quartz, pink and white feldspar phenocrysts, flattened pumice fragments and slate clasts in a quartzo-feldspathic groundmass (Fig. 7). In northern outcrops, the rocks are usually deeply weathered and usually white in colour. Slate clasts are common and vary in abundance throughout the Murtagh Creek Rhyolite. Clasts form less than 2% on the Dart River-Mount Benambra Road and increase with elevation to 30-50% north of Mount Tabor. On Mount Benambra, randomly oriented blocks



Fig. 7—Murtagh Creek Rhyolite consisting of quartz and feldspar phenocrysts and clasts of black slate, Mt. Benambra Road.

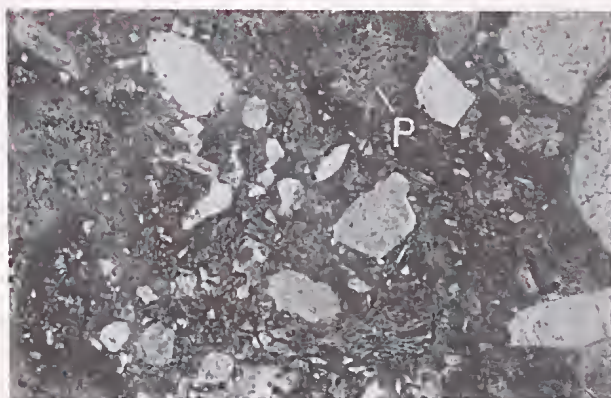


Fig. 8—Rhyodacitic tuff with shard texture and uncompacted pumice fragments (P), Murtagh Creek Rhyolite. ($\times 30$)

of slate and interbedded slate and slate breccia up to 3 m in length occur.

Phenocrysts occupying up to 35% of the rock are mostly bipyramidal and embayed quartz, alkali feldspar and plagioclase, chloritised biotite and small amounts of hornblende. Potash-feldspar is usually more abundant than plagioclase. The groundmass usually displays recognisable devitrified glass shards (Fig. 8) which are often distorted around phenocrysts and clasts. Spherulites occur in isolated pockets and post-date distortion of the shards. Some sections show recrystallisation to a fine grained quartz-feldspathic groundmass which is occasionally chloritic and rarely contains axiolites. Highly cleaved clasts of slate, one piece of "graphitic" slate and occasional quartz sandstone form clasts observed in thin section. One floater of andesite containing euhedral pyroxene phenocrysts in a very fine grained black groundmass was found at Mount Cravensville but its source bed was not located. A thin basaltic unit is exposed in a road cutting near the summit of Mount Benambra. No other basic to intermediate volcanic rocks were found in the Murtagh Creek Rhyolite.

Boundary Relations: The Sheevers Spur Rhyodacite has a complex, faulted eastern boundary against Ordovician metasediments and the Cravensville Formation. The western boundary along the Mitta Mitta River near Eight Mile Creek is intruded by a coarse-grained granite. A complex linear belt approximately 500 m wide along the eastern side of the Mitta Mitta River is exposed along the road between Sheevers Point and Larsen Hill. The Sheevers Spur Rhyodacite here contains a large number of randomly oriented blocks of slate, some greater than 10 m wide (containing Late Ordovician graptolites at three localities), sandstone and knotted phyllite set in a volcanic matrix similar to the rhyodacites of the Sheevers Spur Rhyodacite. It is considered to be a brecciated phase of the Sheevers Spur Rhyodacite but differs from the Dart River Volcanic Breccia in its predominance of metasediment blocks over igneous material.

Talent (1965) stated that the volcanics near Larsen Hill post-date the Bannimboola Diorite because of the

presence of "house-sized blocks" of diorite included in the volcanics. However, these exposures are outcrops of foliated granodiorite, suggested to be a biotite bearing phase of the Eustace Creek Granodiorite, not Bannimboola Quartz-Diorite. There is no conclusive evidence that they are allochthonous blocks. Thin veins of volcanics intrude the granodiorite and there are blocks of biotite granite in the volcanics. The Sheevers Spur Rhyodacite may rest on an irregular erosion surface of the Eustace Creek Granite. The contact is now complicated by faulting.

The relationship between the Bannimboola Quartz-Diorite and the Sheevers Spur Rhyodacite is not clearly established as there are no positively recognised clasts of diorite in the rhyodacite. However, the granite which intrudes the volcanics on the Mitta Mitta River near Eight Mile Creek may be a marginal phase of the Bannimboola Quartz-Diorite, suggesting that the volcanics pre-date the intrusion. The Sheevers Spur Rhyodacite is itself intruded by a quartz-muscovite granite near the junction of Larsens Creek and the Mitta Mitta River and at Larsen Hill.

In the southern outcrops of the Dartella Volcanic Group, there appears to be a gradation from the Sheevers Spur Rhyodacite into the Murtagh Creek Rhyolite, implying a vertical gradation from a more intermediate to more acid sequence. In the northern areas of outcrop, Murtagh Creek Rhyolite unconformably overlies Ordovician slate and higher grade metamorphic rocks and in the Cravensville area the contact appears to be flat lying.

In the headwaters of Murtagh Creek, there are abundant floaters of massive quartzitic sandstone and brown siltstone associated with the Murtagh Creek Rhyolite. Outcrops in this area are poor and it is not known whether the sediments are sedimentary clasts weathered out of the volcanics, are interbedded with the volcanics, or are incorporated into a series of fault slivers aligned parallel to the eastern boundary of the volcanics. There is a large belt of Ordovician metasediments south of Mount Benambra.

Age: The Dartella Volcanic Group post-dates the Benambran Deformation as it contains clasts of sedimentary, igneous and metamorphic rocks deformed by or produced during this event. The Murtagh Creek

Rhyolite is petrographically similar and has similar structural attitude to the Early Devonian Snowy River Volcanics described from southeast of Dartmouth by Ringwood (1955) and the Jemba Rhyolite (Edwards & Easton 1938, Birch 1978) from near Corryong, which has been Rb/Sr dated at 400 ± 8 m.y. (Brooks & Leggo 1972, recalculated by Richards & Singleton 1981). Although there is no certainty that volcanism was contemporaneous in all areas, it is noteworthy that extensive acid volcanism took place in eastern Victoria in the Early Devonian. On this basis it is suggested that the Murtagh Creek Rhyolite may also be of Early Devonian age. The apparent gradation from the Sheevers Spur Rhyodacite to the Murtagh Creek Rhyolite implies that the Sheevers Spur Rhyodacite is also Early Devonian in age.

INTRUSIVE ROCKS

DARTMOUTH GRANITE

Field Character

The Dartmouth Granite is a grey two-mica granite exposed over 11 km² in and around the Dartmouth Dam. It is heterogeneous in texture consisting of medium to coarse grained foliated and non-foliated components (Fig. 9). The foliation is defined by alternating layers of K-feldspar and biotite rich bands.

Xenoliths and biotite-rich schlieren are common throughout the intrusion. Xenoliths are always metasedimentary with two common types. Most common are schistose biotite-quartz-muscovite-potash feldspar-sillimanite (\pm cordierite) xenoliths of pelitic parentage but there are also large (up to 1 m) ovoid quartz-plagioclase-clinopyroxene (\pm actinolite \pm garnet) types which probably represent the quartz-rich limey facies mentioned above. The trend of the foliation and orientation of xenoliths in the Granite parallels the trend of bedding in the enveloping metamorphic rocks, which may imply a close relationship between deformation and intrusion. The northern, western and eastern granite margins are relatively straight, suggesting steep boundaries in those areas. A schistose aureole extends 1.5 km north of the intrusion. Along its southern boundary, it is intruded by the Bannimboola Quartz-diorite (see below), a chemically and petrographically distinct pluton. At least two diorite dykes intrude the Dartmouth Granite just west of the dam. Intrusion of the Bannimboola has locally hornfelsed the previously schistose metamorphics surrounding the Dartmouth mass where the two intrusions are adjacent. Rogerson (1979) has described metamorphic textures imposed on the Dartmouth Granite adjacent to the Bannimboola intrusion.

Mineralogy and Chemistry

Modal analyses indicate approximately 30% quartz, 30% orthoclase, 15% plagioclase, variable (8%-24%) biotite, 3% muscovite and variable accessories (3%). Accessories include cordierite, sillimanite (fibrolite), apatite and zircon. Within 100 m of its boundary with the Bannimboola Quartz-Diorite, the Dartmouth Granite shows sericitised potash feldspar anhedral, biotite altered to chlorite and magnetite and extensive

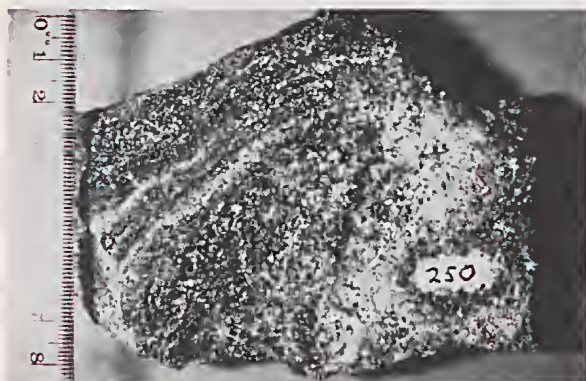


Fig. 9—Foliated and non-foliated components of the Dartmouth Granite.

fibrolite nucleation on biotite. Only one chemical analysis has been carried out on the intrusion (Table 1).

TABLE 1
CHEMICAL ANALYSIS AND CIPW NORM OF DARTMOUTH
GRANITE

SiO ₂	72.11	Quartz	44.21
Al ₂ O ₃	14.42	Orthoclase	21.41
Fe ₂ O ₃	0.97	Albite	12.83
FeO	3.19	Anorthite	1.95
MnO	0.04	Corundum	7.28
MgO	1.52	Hypersthene	8.00
CaO	0.56	Magnetite	1.41
Na ₂ O	1.52	Ilmenite	1.06
K ₂ O	3.62	Apatite	0.30
H ₂ O ⁺	1.66		
H ₂ O ⁻	0.26		
TiO ₂	0.56		
P ₂ O ₅	0.13	Anal. R. Rogerson	
	100.56		

The analysis shows low CaO typical of *S-type* granites (Chappell & White 1974) and relatively high SiO₂ and Al₂O₃.

Age: The Dartmouth Granite pre-dates intrusion of the Bannimboola Quartz-Diorite. Similar granites with schistose aureoles comprising parts of the Corryong Batholith further north have Rb/Sr ages of 421 ± 8 m.y. (Brooks & Leggo 1972, recalculated by Richards & Singleton 1981). The Dartmouth Granite is considered on regional grounds to be of Early Silurian age.

EUSTACE CREEK GRANODIORITE

The Eustace Creek Granodiorite was exposed along the Mitta Mitta River prior to inundation by the Dartmouth Dam. It has been regarded as an eastern phase of the Bannimboola Quartz-Diorite (Talent 1965, Singleton 1965, Modrich 1973) but recent work suggests that it is an older, multi-phase intrusion which is being deroofed at present. A foliated, medium-grained deformed quartz-diorite consisting of quartz and plagioclase, abundant fragmented green hornblende and kinked chlorite (probably after biotite) outcrops on the Mitta Mitta River near the mouth of Eustace Creek. The rock is intersected by veins of (?) epidote and there is extensive plagioclase alteration. Granitic rocks outcropping along Larsen Creek and exposed in road cuttings near Larsen Hill are also included in the Eustace Creek Granodiorite. At Larsen Hill, there is a coarse grained foliated granodiorite containing quartz, plagioclase, minor potash feldspar, chloritised biotite and highly altered hornblende. In contrast to the outcrop at the mouth of Eustace Creek, biotite is the major mafic mineral in the Larsen Hill exposure. Gradations between the two rock types described above, including some unfoliated phases, outcrop along the Mitta Mitta River

north of Eustace Creek. No xenoliths have been observed.

The Eustace Creek Granodiorite intrudes Ordovician metasediments along the Mitta Mitta River, where the top of the intrusion is exposed in cliffs. In the complex brecciated zone in the Sheever Spur Rhyodacite, thin veins of volcanics similar to the Sheevers Spur Rhyodacite penetrate the Granodiorite. If the suggested Early Devonian age of the volcanics is correct, the Eustace Creek Granodiorite must be older than Devonian.

A K/Ar date of 440 ± 9 m.y. has been obtained for hornblende from an outcrop on the Mitta Mitta River (Richards & Singleton 1981). Another K/Ar date of 388 ± 8 m.y. was obtained by AMDEL using specimens from the same outcrop. However, the hornblendes used in the latter case contained carbonate. The older date of 440 ± 9 m.y. may therefore be more reliable and suggests an Early Silurian age for the Eustace Creek Granodiorite.

SOUTHERN GRANITES

Two intrusions observed in the southern part of the Dam area are referred to informally as "The Southern Granites" and require more detailed study. Their intrusive relationships to the Upper Silurian Wombat Creek Group indicates a probable Early Devonian age.

Tonalite at Taylors Crossing

A small elongate intrusion outcropping in the valley of the Mitta Mitta River near Taylors Crossing is a medium-grained grey tonalite comprising quartz, plagioclase, abundant biotite and some muscovite. Locally, it is foliated and contains randomly oriented micaceous xenoliths. It appears to intrude the Wombat Creek Group on the Mitta Mitta River, although the contact is not well exposed.

Granite on the Lower Tableland

A deeply weathered and poorly exposed intrusion in the Lower Tableland area, north of Benambra, has contact metamorphosed the Upper Silurian Wombat Creek Group. It is fine to medium grained granite containing perthitic orthoclase, oligoclase, quartz, biotite and pinitised cordierite (Crohn 1950) and some primary muscovite. Dykes associated with this intrusion outcrop along the Mitta Mitta River.

BANNIMBOOLA QUARTZ-DIORITE

Field Character

The Bannimboola Quartz-Diorite is exposed in an irregular shaped mass over 130 km² from Dartmouth to Granite Flat. A 1 km wide contact aureole has porphyroblasts of andalusite, cordierite, biotite and, within 20 m of the contact, sillimanite, overprinting regional chlorite-bearing slates. Near Dartmouth it intrudes the Dartmouth Granite. It is separated from the Dartella Volcanic Group by granitic rocks along Eight Mile Creek. In outcrop, the diorite is greenish-grey, lacks foliation and is generally homogeneous. It is often weathered, with large extremely tough, rounded tors in a

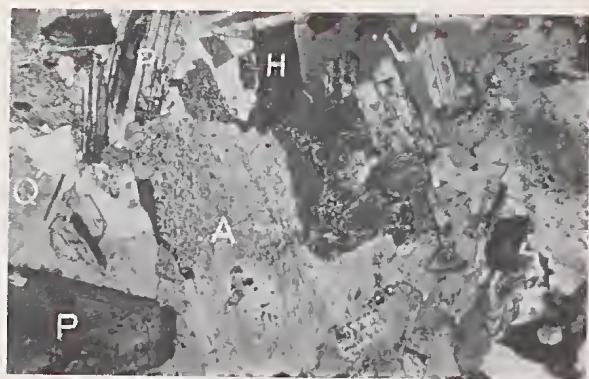


Fig. 10—Photomicrograph of Bannimboola Quartz-Diorite showing tabular augite (A), hornblende (H) and plagioclase (P) with interstitial quartz (Q). ($\times 30$)

residual feldspathic clay soil, although it does form rugged topography which reaches 1100 m at Granite Peak. Xenoliths up to 10 cm are locally abundant and commonly have diffuse boundaries. Most are amphibolitic with plagioclase-hornblende-clinopyroxene assemblages. Except within 1 m of its boundaries, the intrusion has no metasedimentary xenoliths.

Mineralogy and Chemistry

Grain size of the intrusion ranges from 1 mm to 3 mm. In thin section, it consists principally of subhedral plagioclase, hornblende, biotite and clinopyroxene phenocrysts (Fig. 10). Minor potash feldspar and quartz are interstitial. Scattered altered pinkish orthopyroxene anhedrala are present in some sections. Sphene and apatite are accessory. In places, pigeonite is present. Modal analyses are presented below (Table 2). Several chemical analyses on the diorite have been carried out (Table 3) and a CIPW norm is shown for Analysis 1.

Points to note about these analyses include: a, relatively low SiO_2 , K_2O relative to the Dartmouth Granite; b, abundant FeO , MnO , MgO , and Ca ; c, $\text{Na}_2\text{O} > \text{K}_2\text{O}$ (except analysis 3). These chemical variations are reflected in the norm where diopside is present

TABLE 2
MODAL ANALYSES OF BANNIMBOOLA QUARTZ-DIORITE

	1	2	3
Quartz	13.5	12.5	10.0
Alkali Feldspar	21.5	5.0	8.0
Plagioclase	48.0	35.0	40.0
Hornblende	9.5	25.0	20.0
Clinopyroxene	4.5	12.5	11.5
Biotite	1.0	5.0	8.0
Orthopyroxene	—	3.0	1.5
Accessories	2.0	2.0	1.0

(1) GR 53984863 Benambra 1:100 000

(2) GR 54684894 Benambra 1:100 000

(3) GR 54504813 Benambra 1:100 000

TABLE 3
CHEMICAL ANALYSES AND CIPW NORM OF BANNIMBOOLA QUARTZ-DIORITE

	1	2	3
SiO_2	59.64	58.60	60.60
Al_2O_3	14.35	14.30	13.60
Fe_2O	3.17		
FeO	4.18	6.70	6.20
MnO	0.67	0.13	0.10
CaO	6.60	7.10	7.50
MgO	4.27	4.40	6.40
Na_2O	2.95	2.70	2.70
K_2O	2.14	2.40	2.80
H_2O^+	1.41	ND	ND
H_2O^-	0.24	ND	ND
TiO_2	0.71	0.60	0.50
P_2O_5	0.12	0.10	0.10
CO_2	*	ND	ND
	100.45	97.03	100.50

Quartz	14.44
Orthoclase	12.68
Albite	24.94
Anorthite	19.54
Diopside	10.06
Hypersthene	10.93
Magnetite	4.59
Ilmenite	1.07
Apatite	0.28

(1) Bannimboola Quartz-diorite, Anal. R. Rogerson

(2) Bannimboola Quartz-diorite (Hesp 1974: 23)

(3) Bannimboola Quartz-diorite (Hesp 1974: 24)

and corundum absent. Hesp (1974) has reported high trace copper values (40 and 200 ppm) for this intrusion. The analyses above, and the presence of meta-basic (intermediate) cognate xenoliths in the intrusive, together classify it as an *I-type* granite (Chappell & White 1974).

Age

The Bannimboola Quartz-diorite has intruded the Dartmouth Granite and post-dates major regional ductile deformation of Ordovician metasediments. K/Ar age determinations on the pluton ranging between 399 ± 16 and 409 ± 16 m.y. (Richards & Singleton 1981), imply an Early Devonian cooling age for the diorite. This age is also significant as it suggests that the Dartella Volcanic Group and the diorite may be temporally related. Further chemical/isotopic work would be required to relate the diorite to the volcanics in a sub-volcanic/volcanic sense.

GRANITE AT EIGHT MILE CREEK

A coarse-grained unfoliated, irregularly porphyritic granite outcrops occasionally on the Mitta Mitta River and in the Eight Mile Creek catchment area. It intrudes volcanics of the Dartella Volcanic Group (Bolger & Rogerson 1978b) at G.R.496519 but its boundary with the Bannimboola Quartz-Diorite is not exposed. Its

petrography has not been studied in detail. Where it intrudes the Sheevers Spur Rhyodacite it is a coarse grained plagioclase-quartz-potash feldspar-hornblende granodiorite. Chlorite occurs in patches and aggregates and may be replacing biotite. Fifty metres downstream from the Volcanics boundary, abundant medium-grained dioritic xenoliths occur. Adjacent to the Volcanics boundary, the granite contains accidental xenoliths of the Volcanics and occasional pyrite cubes. In the Eight Mile Creek catchment, this granite is rich in biotite and often lacks hornblende. The overall outcrop pattern, mineralogy and cognate xenolith population of this granite suggests it is similar to the Bannimboola Quartz-Diorite and they may be part of the same intrusive cycle.

The Granite at Eight Mile Creek shows many similarities to the Eustace Creek Granodiorite. Both of these bodies are highly complex intrusions which occupy similar structural settings marginal to the main volcanic belt of the Sheevers Spur Rhyodacite. They are poorly exposed, of variable grain size and texture and comprise a variety of rock types, all containing biotite and variable amounts of hornblende. However, the Eustace Creek Granodiorite on the east appears to be older as it is intruded by, and forms inclusions in, the Sheevers Spur Rhyodacite. In contrast, the Granite west of the Volcanic Belt at Eight Mile Creek contains clasts of the Volcanics and is a marginal intrusion. Foliation is also common in the Eustace Creek Granodiorite but was not observed in the western granite at Eight Mile Creek. Foliation alone as a criterion for distinction must be treated with caution as the foliation in the Eustace Creek Granodiorite may be related to its proximity to the roof of the intrusion.

MUSCOVITE GRANITES

A fine to very coarse grained leucocratic muscovite granite covers wide areas near Eight Mile Creek and Eustace Creek. It is highly weathered, outcrops are rare, and the material available was unsuitable for thin section. In hand specimen, it appears to contain quartz-feldspar-muscovite and some tourmaline. It intrudes the Eustace Creek Granodiorite downstream from the mouth of Eustace Creek and the Sheevers Spur Rhyodacite near Larsen Hill. West of the volcanic belt the muscovite granite appears to intrude the Dartmouth Granite, the Bannimboola Quartz-Diorite and the granite at Eight Mile Creek.

SUB-VOLCANIC QUARTZ PORPHYRIES

There are a number of massive, pink quartz and quartz-feldspar porphyritic rocks exposed adjacent to the Wombat Creek Graben. A large massive body intrudes the Cravensville Formation in a creek north of Mount Benambra. Large dykes of similar composition intrude Ordovician metasediments along the Dart River upstream from Vincent Creek, and west of the Sheevers Spur Rhyodacite near Eight Mile Creek there is a poorly exposed quartz porphyry.

The intrusive relationships of all of these bodies are not clearly established but they are presumed to repre-

sent sub-volcanic rocks associated with the intrusion of the volcanics. Similar "granite porphyries" in the Gibbo River area to the south may have affinities with Siluro-Devonian volcanics in the Wombat Creek Graben rather than with the Triassic Mt. Leinster Complex which outcrops in the Benambra area to the south of the Dam.

DEFORMATION AND METAMORPHISM

SILURIAN DEFORMATION

Metamorphism

The regional metamorphic rocks described above as medium and high grade Ordovician metasediments are schistose rocks occurring as aureoles around the Dartmouth Granite and Eustace Creek Granodiorite. This style of metamorphism is found throughout the Omeo and Wagga Metamorphic belts and results from the intrusion of granitic magmas during regional deformation. Cordierite and/or andalusite at medium grades, absence of kyanite and the incoming of alkali-feldspar soon after sillimanite in prograde metamorphism suggest the metamorphism was low pressure. Close association of granites and metamorphism implies the latter was Early Silurian in age.

Deformation

Detailed description of Ordovician metasediment deformation features is beyond the scope of this paper. Detailed descriptions and geometrical interpretation of Ordovician structures in this and surrounding areas are presented in Beavis and Beavis (1976), Rogerson (1976, 1979), Hellman (1976) and Fagan (1979). Two periods of regional ductile deformation occurred in the map area (Rogerson 1979). The first, D_1 , produced upright to steeply inclined non-plunging or shallow plunging tight to isoclinal mesoscale folds with a well developed sub-vertical axial plane slaty cleavage (S_1). Little is known of the strike of axial surfaces.

These folds were overprinted by upright 150° trending, plunging to reclined regional D_2 antiforms and synforms with an axial plane cleavage (crenulating S_1) developed in their hinge areas. The cleavage appears to be absent on fold limbs where strain occurred on S_1 cleavage planes. This second deformation led to rapid changes in younging and dip directions within Ordovician metasediments. Two contrasting D_2 fold styles are present in Ordovician metasediments separated on the map sheet by the Wombat Creek Graben. West of the Graben, the open to tight, steeply plunging (almost reclined) Callaghans Creek Synform (Rogerson 1979) occurs. On the Mitta Mitta-Dartmouth Road, D_1 mesofolds on the western limb of the D_2 synform are well developed. The regional synformal hinge area is traversed on the Dartmouth-Mt. Benambra Road. East of the Graben, no macrofolds of bedding have been described north of the Gibbo River. Isoclinal steeply plunging to reclined D_2 folds occur in this area so that most bedding and S_1 strike 150° . Ordovician metasediments strike easterly in the sedimentary corridor near Soldier Creek and in small areas along the Gibbo River.

WOMBAT CREEK GROUP AND MITTA MITTA VOLCANICS DEFORMATION

The Wombat Creek Group is tightly to isoclinally folded on gently plunging to horizontal hinge lines trending 150° which are parallel to folds in adjacent low grade Ordovician metasediments. A vertical reticulate cleavage parallels fold hinge surfaces.

Folding of the Mitta Mitta Volcanics has been determined from the orientation of columnar joints and a tuffaceous sediment bed along the Mitta Mitta River. Dips are steep but younging directions are uncertain. A dip variation from steeply SW, near the confluence of the Gibbo and Mitta Mitta Rivers, to easterly near Italian Point, may be due to faulting, folding or a combination of both. General trends in the Mitta Mitta Volcanics parallel Wombat Creek Group trends. Deformation of Wombat Creek Group and the Mitta Mitta Volcanics is assigned to the Late Silurian to Early Devonian Bindian Deformation prior to extrusion of the Dartella Volcanic Group.

DARTELLA VOLCANIC GROUP DEFORMATION

The Dartella Volcanic Group appears to be gently tilted or folded into broad open folds. Occasional dips, measured on eutaxitic foliation in the Sheevers Spur Rhyodacite, are generally less than 30° . The base of the Murtagh Creek Rhyolite in the Mt. Cravensville and Lightwood areas follows the topographic contours and suggests that the sequence is flat-lying. Adjacent to the margin of the Group, especially in the Cravensville Formation, some steep dips probably reflect movement on boundary faults. In the Dart River area, the attitude of the Dart River Volcanic Breccia varies widely and is complicated by widespread faulting.

FAULTS

The Wombat Creek Graben is bounded by major faults which were probably active during deposition of the Silurian to Devonian sequences in the Graben.

In the southern parts of the Graben, the Silurian Mitta Mitta Volcanics and Wombat Creek Group are bounded by the Wombat Creek and Morass Creek Faults which may have displacements greater than 3000 m. Near Limestone Gap, the Wombat Creek Fault has a wide crush zone, although further south the crush zone is absent and the fault is more difficult to locate. To the south, the Wombat Creek Fault is truncated by the Morass Creek Fault which continues southwards to Benambra. To the north, the Wombat Creek Fault appears to split into a number of faults juxtaposing the Mitta Mitta Volcanics and the Wombat Creek Group. The Morass Creek Fault continues to the north-west along Larsen Creek where contact metamorphic rocks of the Eustace Creek Granodiorite have been faulted out. Near Eustace Gap, it truncates the Soldier Creek Fault and forms the eastern boundary of the regional metamorphic zone along Eustace Creek.

Ordovician high grade metasediments are faulted against Mitta Mitta Volcanics by the east-west trending Soldier Creek Fault which forms the northern boundary

of the Silurian sequence. Along the Mitta Mitta River, there is a 100 m wide crush zone and along the Eustace Gap Track, distorted slate and recrystallised volcanics occur in the fault zone.

Near Larsen Hill and Sheevers Point, the Sheevers Spur Rhyodacite and Ordovician metasediments are strongly distorted by the Larsen Hill Fault. Numerous fault planes can be seen in road cuttings. The Larsen Hill Fault forms the eastern boundary to the Rhyodacite along the Sassafras Gap Track. The eastern boundary of the Murtagh Creek Rhyolite is faulted against Ordovician metasediments by the Murtagh Creek Fault with much shearing of both volcanics and sediments. The Murtagh Creek Fault continues from the Glamour Hill Track to the junction of Shady Creek and the Dart River where the local structure is highly complex.

South of Mt. Benambra, a northeast to southwest trending belt of low grade Ordovician metasediments appears to be faulted against the Murtagh Creek Rhyolite and Sheevers Spur Rhyodacite on its southern side. The fault trends to the southwest towards the Mitta Mitta River but is not recognised at the river where there is an intrusive contact between the Sheevers Spur Rhyodacite and the granite near Eight Mile Creek. However, the distribution of younger intrusions and the linear nature of the western boundary of the Sheevers Spur Rhyodacite south of the river suggests that the boundary has been governed by a major structure which formed the margins of the Graben. Similarly, the western boundary of the Murtagh Creek Rhyolite and Cravensville Formation near Mount Tabor is considered to be faulted and movement on the fault has produced the steep dips in the Cravensville Formation.

The faulted boundary between the Murtagh Creek Rhyolite and Ordovician metasediments on the Dartmouth to Mt. Benambra Road is marked by the abundance of pegmatite veins. The fault trends northwest and follows the trend of the Morass Creek Fault beneath the Sheevers Spur Rhyodacite, although it has not been identified within the Rhyodacite. Faults and shear zones trending northwest to southeast are abundant at the Dam site in the Dartmouth Granite and the surrounding metamorphics. Major regional structures displacing regional metamorphic rocks in the north of the area are the Tallangatta Creek and Dribbling Creek Faults. They are recognisable over distances of tens of kilometres to the north but cannot be traced into the volcanic rocks of the Dartmouth area.

EARLY PALAEOZOIC GEOLOGICAL HISTORY

Deposition of terrigenous sediments in the Wagga Trough occurred from the Early to Late Ordovician. There is no record of Early Silurian sedimentation in this area although evidence from the Yalmy area to the east suggests that sedimentation continued uninterrupted from the Ordovician to the Early Silurian (VandenBerg *et al.* in press). Sometime in the Early Silurian, an event referred to as the Benambran Deformation produced intense deformation, metamorphism and generation of acid magmas, resulting in the forma-

tion of the Omeo Metamorphic Complex and its outlier at Dartmouth.

In the (?) Middle Silurian, the Wombat Creek Graben developed, initiating the extrusion of the Mitta Mitta Volcanics. The volcanism was followed by marine transgression and deposition of the Wombat Creek Group. Late Silurian to Early Devonian folding of the Silurian sequence was followed by acid to intermediate sub-aerial volcanism now preserved in the northern parts of the Graben as the Dartella Volcanic Group. Diorite, granodiorite and muscovite-bearing granitic rocks intruded the older metamorphic and igneous complexes. Mild tilting of the Dartella Volcanic Group took place in the Middle Devonian Tabberabberan Deformation. The margins of the Graben and attitudes of units within the Graben have subsequently been modified by faulting.

ACKNOWLEDGEMENTS

We wish to thank I. A. Nicholls, R. A. Cas, and O. P. Singleton for supervision of parts of the project and C. J. L. Wilson, S. D. Beams, A. H. M. VandenBerg, L. M. Chenoweth and J. R. Richards for discussion of aspects of the petrology, stratigraphy and structure of the area. W. D. Birch and the late D. T. Currey read and commented on the manuscript. This paper is published with the permission of the State Rivers and Water Supply Commission and the Director of the Geological Survey of Victoria.

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SHORT COMMUNICATIONS

OCCURRENCE OF THE COPEPOD PARASITE *LERNAEA CYPRINACEA* L., ON THE AUSTRALIAN GRAYLING, *PROTOTROCTES MARAENA* GÜNTHER

The Australian grayling *Prototroctes maraena* is the only extent member of the family Prototroctidae (McDowall 1976); the only other species, *P. oxyrhynchus*, is presumed to be extinct (McDowall 1976). Although the actual status of *P. maraena* within southeastern Australia remains uncertain (Bell *et al.* 1980), it is evident that existing populations are scarce. This situation has existed for over 100 years (McDowall 1976) and is undoubtedly responsible for the scant knowledge regarding the life history of the species. Recent contributions by Jackson (1976) and Bishop & Bell (1978) have elucidated many aspects of the biology of *P. maraena*, but to date there have been no reports relating to parasites on this species (Beumer *et al.* 1982). In this paper I report the discovery of the anchor worm *Lernaea cyprinacea* on specimens of *P. maraena* taken from the Tambo River in Gippsland, eastern Victoria.

MATERIALS AND METHODS

Specimens of *P. maraena* were collected from the Tambo River in the vicinity of Playgrounds Road bridge during May, 1982. The fish were taken from a 200 m section of the river by rotenone poisoning. Caudal fork lengths (LCF) of all specimens taken were measured to the nearest millimetre and sex determination made by macroscopic examination of the gonads. Specimens were frozen and returned to the laboratory within one week.

Examination by eye enabled the number of transformed female *L. cyprinacea* (see Nakai 1927) together with their respective positions on each fish to be determined and recorded. The number and position of lesions were also recorded as they indicate either those areas of penetration where the females are not visible by macroscopic examination, or those areas from which the parasite had recently been dislodged (Robinson 1982). The gills of each fish were rinsed in 10% formalin and examined for non-transformed life stages of the parasite. All other fishes taken were examined in the same way for both transformed and non-transformed copepod life stages.

RESULTS

Of 9 (7 males and 2 females) specimens of *P. maraena* collected, with a size range of 117 to 231 mm length, three carried transformed female *Lernaea* and/or lesions. A female 231 mm long had one *Lernaea* and a lesion near the base of the dorsal fin and another lesion on the body dorsal to the lateral line. A male 207 mm long had 3 *Lernaea* on the dorsal fin and 2 *Lernaea* as well as a separate lesion dorsally on the body. Another male 117 mm long had a single lesion on the dorsal fin. A total of 6 transformed *L. cyprinacea* were found ranging in length from 8.5 to 12.5 mm (Mean=10.6; SD=1.57). Five of the specimens possessed egg sacs containing many well developed eggs. An examination of the gills of the grayling specimens failed to reveal any non-transformed life stages of the parasite.

Other fish species taken were tumpung, *Pseudaphritis urvilli* (Cuvier & Valenciennes) (n=2, LCF 79-208 mm), Australian smelt, *Retropinna semoni* (Weber) (n=37, LCF 33-67 mm) and the common galaxiid, *Galaxias maculatus* (Jenyns) (n=40, LCF 79-122 mm). Examination of these fishes showed a total absence of all life stages of the parasite.

The water temperature ranged from 8.5 to 11.0°C during the two week period prior to sampling—conforming with the

pattern from historical records for nearby Ramrod Creek kept by the State Rivers and Water Supply Commission of Victoria, Melbourne.

DISCUSSION

Lernaea cyprinacea is capable of causing considerable losses to fish populations, particularly in intensive culture ponds (Lahav & Sarig 1964, Lahav *et al.* 1964, Meyer 1966). Levels of infection in flowing streams are significantly lower as a result of water movement (Bulow *et al.* 1979). The potential for heavy infections of *L. cyprinacea* during the spawning activity of *Prototroctes maraena* in late autumn (B. R. Tunbridge pers. comm.) seems unlikely. The life cycle of *L. cyprinacea* is highly dependent on temperature (Nakai & Kokai 1931, Shields & Tidd 1968) with the strain present in Australia requiring a temperature of 24°C to complete its life cycle (Robinson 1982). Daily temperatures in the Tambo River during the period in which the grayling spawn rarely exceed 15°C—which is insufficient for the hatching and transmission of parasite larvae to occur. The parasite specimens found during this study presumably constitute the over-wintering population (*sensu* Nakai & Kokai 1931). Further evidence for this assumption is provided by the absence of non-transformed parasites on the gills of the grayling.

The location of spawning of *P. maraena* has long been a matter of conjecture. Johnston (1891) and Lord & Scott (1924) promulgated the view that grayling migrate downstream to brackish water to spawn, whilst Bishop & Bell (1978) suggested that the species spawns in freshwater. *L. cyprinacea* may now provide an intermediate in determining the location of spawning for grayling. Shields & Sperber (1968) found that the posterior region of the parasite, including the egg sacs, is susceptible to the osmotic concentration of the external medium and that eggs exposed to salinities greater than 3 ppt became malformed or amorphous. As the over-wintering parasite population in the Tambo River possess egg sacs, future observations on the state of the eggs on parasites infesting spent grayling would be useful in determining the spawning area of *P. maraena*. Malformed eggs on *L. cyprinacea* infesting spent grayling would indicate that the fish had been in brackish water, whereas normal well-developed eggs on the parasite would suggest that the grayling had spawned in freshwater.

This is the first time *L. cyprinacea* has been reported south of the Great Dividing Range in Victoria and represents a significant transition for the parasite into relatively cooler coastal waters.

ACKNOWLEDGEMENTS

I am grateful to Ms G. Newton (University of Melbourne) for confirming the identification of the copepods and to Mr B. R. Tunbridge, Mr. T. Glenane and Mr B. O'Connor for assistance during specimen collection. Constructive criticisms of the manuscript were kindly provided by Dr J. P. Beumer, Mr B. R. Tunbridge and Mr J. H. Pribble.

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A NEW LATE SILURIAN THALLOPHYTE FROM CENTRAL VICTORIA

Tims (1978), Tims & Chambers (in press), and Douglas & Lejal-Nicol (1981) provided some insight into the flora of the Lower Plant Assemblage at Limestone Road, near Yea, in central Victoria, contained in beds of the early Palaeozoic Melbourne Trough. Three different algae from this locality were also discussed by Douglas (1981). Unlike other algae recorded from the locality and indeed unlike most fossil plant taxa which are almost invariably isolated organs of a much larger body, this new specimen apparently represents an almost complete plant. It is an addition to the *Baragwanathia* flora, at least half a dozen members of which are regarded as thallophytes; of these only *Yeaia* and *Buthotreplis divaricata* Kidson have been formally named.

Class THALLOPHYTA
Order PHAEOPHYTA?
Family Indeterminate

Genus *Yeaia* nov.

TYPE SPECIES: *Yeaia flexuosa* sp. nov.

DIAGNOSIS: Plant with roots or holdfast. Thallus long, flat and strap-like, repeatedly dichotomising and twisting, arising as major stem or stems 3 mm in width from contorted roots or holdfast. Stem width more or less uniform for 30-50 mm before branching, further branching at greater distance along the thallus. Maximum thallus width 8-10 mm, length at least 300 mm.

Yeaia flexuosa sp. nov.

Figs 1, 2

DIAGNOSIS: As for genus.

HOLOTYPE: NMVP173478.

LOCALITY: Limestone Road, Yea in excavation 10 m from southern end of western (bulldozed) side of cutting. (465088 on Yea 1:50 000 topographical Map no. 7923-1). The specimen is an orange-red impression on light brown-grey siltstone or claystone of the Lower Plant Assemblage of the Yea Formation which has been assigned a Late Silurian (Ludlow) age by Garratt (1978) and was collected in August 1981, by J. G. Douglas and M. J. Garratt.

REMARKS: The fossil represents a plant which may have reached half a metre in height, with long flexuous thallus. The twisting and involution of the thallus 5 or 6 cm above the base may have been accentuated or largely caused by movement and tumbling during deposition, although transport from growth position is envisaged as minimal because of the lack of laceration, absence of thallus damage, and the adhering substrate in the holdfast area. A portion of the thallus is indicated by an arrow in Fig. 2. The attachment area of this is obscure and it is possible that it was derived from a separate plant, but I regard this as unlikely. It is of the same order of size as the attached portion, and so intimately associated as to most likely have originated from the plant under discussion. There is no indication of conducting tissue in the thallus and unfortunately fertile organs also seem to be absent.

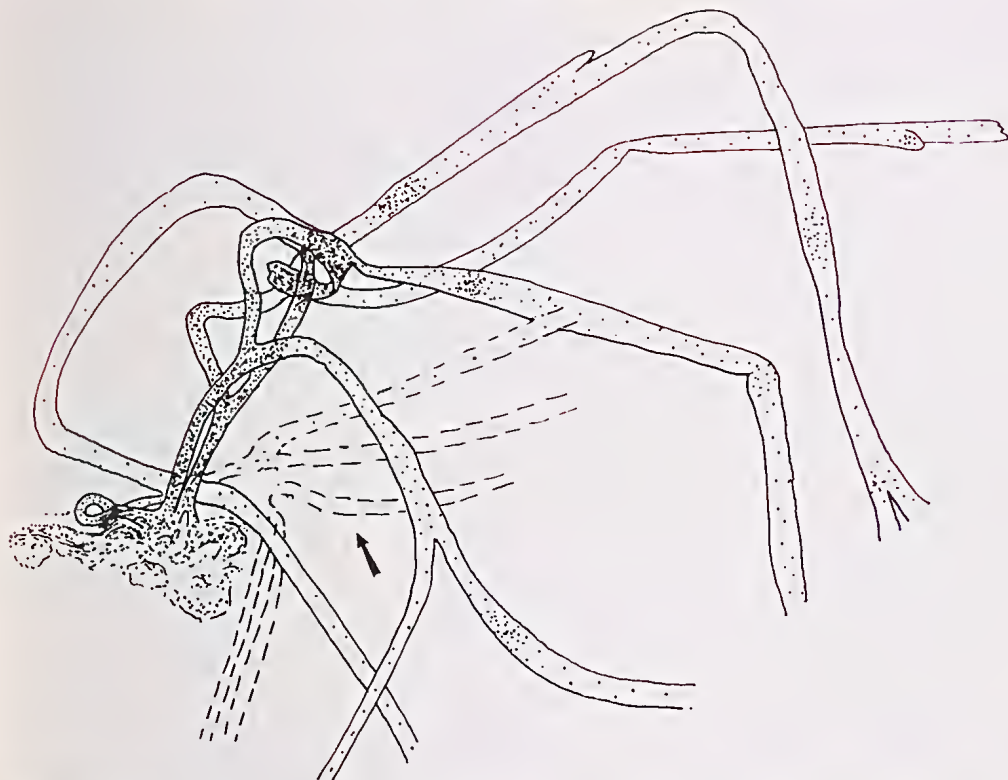


Fig. 1—*Yeaia flexuosa* sp. nov. Line drawing of counterpart of holotype showing thallus form, NMVP173478, $\times 0.5$.



Fig. 2—*Yeaia flexuosa* sp. nov. Holotype, NMVP173478, $\times 1$.

AFFINITY: Plant form strongly suggests affiliation with the Thallophyta and relationship to the fucoids immediately comes to mind, although algal specialists will no doubt see similarities to other present day phaeophytes and possibly to some rhodophytes.

Taggart & Parker (1976) commented that 'impressions and compressions resembling thalli of modern brown algae (Phaeophyta) are relatively common in Palaeozoic marine deposits' . . . , but I can find no record of fossils like this specimen. *Buthotrephis* species described by Lucas (1927) and others from various localities in the Melbourne Trough should be among the first to be compared. However, the *Buthotrephis* plant seems to have been much smaller and although the thallus branches dichotomously, it is much finer than *Yeaia*.

Fry and Banks (1955) described an alga (*Hungerfordia dichotoma*) with dichotomising thallus, but this was much smaller, and with swollen, not strap-like branches. These authors also remarked that 'some (Devonian) algae might show many characteristics not found in living algae,' but I still maintain the likelihood of affiliation with the phaeophytes.

PALAEOENVIRONMENT: The Yea Formation was laid down in the entirely marine Melbourne Trough and the well preserved condition of the specimen with substrate still adhering is, as already remarked, taken to indicate '*in situ*' or near '*in situ*' fossilisation. If this occurred in shallow water or the tidal zone this would conflict with the deep sea environment postulated by Garratt (1983).

ACKNOWLEDGEMENTS

I thank Dr. J. D. Tims for manuscript criticism, and Miss Christine Donohoe for the photograph. This communication is published with the permission of the Director, Geological Survey of Victoria.

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THE MOONLIGHT HEAD ROCKSHELTER

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ABSTRACT: An aboriginal midden located at the base of sandstone and shale cliffs near Cape Otway, southwestern Victoria, was excavated in 1980. It contained evidence of occupation of the coast for approximately 1000 years prior to the contact period. The midden deposit consisted mainly of the remains of shellfish, but also contained animal bones and stone artefacts. Analysis of the shellfish revealed a shift in exploitation from the larger species, which are more difficult to harvest, to use of the smaller though more easily gathered animals. Study of the number of animals represented by the vertebrate remains, and calculation of the density of material, indicates that this shift is associated with increased exploitation of the land fauna in later periods of occupation. Finally it is suggested that this is indicative of a change in the logistical pattern of land use in the Otway region.

Moonlight Head Rockshelter was excavated in January and February 1980, in what was envisaged as one of the first steps in a broader study of the Gellibrand River region, aimed at studying coastal and estuarine exploitation strategies, and inland settlement patterns.

THE SITE AND ITS SETTING

Moonlight Head Rockshelter

Victoria Archaeological Survey Site Number 75203/029

County of Polworth, Parish of Wangarrip

Latitude 38°45' 5" S; Longitude 143°13' 15" E

Moonlight Head is one of a number of cliffed promontories which jut out into the sea near the western edge of the Otway Ranges (Figs 1, 2). A few kilometres to the west the cliffs end at the mouth of the Gellibrand River, which forms a large estuarine basin behind the tidal sand-bar dividing it from the sea. Similar estuaries are seen elsewhere in the Otways, as at Glen Aire and Apollo Bay.

The Otway Region can be divided into two basic landforms: 1, the Coastal Plains and 2, the Otway Ranges which rise to a maximum height of 670 m. Moonlight Head lies approximately on the western division between these areas (Douglas 1977: 19). Behind the site the ranges rise to approximately 200 m at 2.5 km inland, falling again to the Gellibrand River some 4.5 km inland.

Annual rainfall ranges from 900 mm on the coast to 1800 mm inland. There is some seasonal fluctuation with most rain falling between May and October (Linthorpe 1977: 61). The mean summer temperature on the coast is about 20°C, and about 13°C in winter (Victoria Land Conservation Council 1976: 32).

Although a considerable proportion of the land has been cleared and used for agriculture—predominantly dairy farming and grazing (V.L.C.C. 1976: 225)—large tracts of land have remained in public ownership. On much of this land, traces of the native vegetation remain.

The Coastal Vegetation Complex generally extends inland for about 1 km or less. The exposed frontal dunes now support a grassland of marram grass, tea-tree scrub (*Leptospermum laevigatum*) and sawlow wattle

(*Acacia longifolia*). This complex gives way to various types of Open Forest (V.L.C.C. 1976: table 7), principally of brown stringybark (*Eucalyptus baxteri*) and messmate (*E. obliqua*). Further into the ranges, as the rainfall increases, mountain ash (*E. regnans*) and blue gum (*E. globulus*) come to predominate, and the undergrowth becomes more dense. In some of the wettest gullies a Closed Forest has developed.

The shore near Moonlight Head is rugged and difficult of access. Behind the sandstone and mudstone cliffs (Douglas 1977: 19), which drop sharply to the sea, are a series of steep rounded hills. Small isolated beaches and rock platforms lie at the base of the cliffs, and are covered by the sea at high tide. Waves rolling against the cliff face have sculptured numerous sea caves.

Coastal archaeological sites—middens and lithic scatters—are normally found on high dunes or cliff tops as, for example, further east at Seal Point near Cape Otway (Lourandos 1980, Bowdler & Lourandos 1982), and at Glen Aire (Stuart 1979). Moonlight Head Rockshelter, however, is unusual in this respect, tucked into the foot of a cliff in a sea-eroded cave, and therefore directly adjacent to the beaches and rock platforms. Sea caves of this kind are daily scoured by tidal waters; indeed, exceptionally high and storm-aggravated tides are active agents in the contemporary destruction of the midden located in Moonlight Head Rockshelter. Alec Neave, who has known the site for over 40 years, can clearly recall when the midden extended perhaps as much as 10 m further to the south. What is left today is only a small part of a once very substantial deposit.

When we first saw the site in 1979 a nearly vertical face of stratified midden deposit over 1.5 m in depth and about 2 m in width was visible near the northwest cliff-wall. On the east, thick, heavy, deposits of sandstone boulders and soil covered further deposits. The more visible western part was also sealed by a massive roof-fall of extremely large sandstone blocks. Other similar blocks lay on the pebble-strewn slope running down from the midden to the sea.

Moonlight Head Rockshelter is not a very effective shelter, because the prevailing winds from the west or southwest blow rain or spray directly into the site, while a constant trickle of sandstone fritters off the high walls.

Water, however, is available from a small perennial creek running over a waterfall and into a catchment on higher ground behind the shelter. This is reached by climbing up and over the high steeply sloping roof-fall currently covering the midden deposit, moving around the eastern curve of the cliff-wall at the rear, and thence over a narrow shoulder of fairly recent slumped soil onto a small flat open space high above the sea. This spot is better protected from the wind and, unlike the midden area, is warmed by the sun. A small test excavation (MLH II) was carried out here (see below).

At present it is possible, although not without some difficulty, to climb a 3 m high face onto the top of the waterfall, and then follow the creek inland up a narrow valley, through thick scrub, or climb a steep slope to the top of the cliff. The site may also be approached from the west, by climbing down a cliff onto an adjacent rock platform. A somewhat safer way to the site is from the east along the rock platforms and beaches after descending a less formidable section of cliff below a steep hillslope. This route, and the western cliff, are nearly impassable when the water is up, and extremely dangerous in a storm. Access to the site, then, is more or less limited to fine weather.

Two main rock platforms lie beside the site. At high tide, or during windy weather, the rock platforms are under water. When the water is low, large flat areas are exposed, with sharp edges dropping off into deep water. Except on rare calm days the water is rough, and diving off these platforms would always have been hazardous.

In summary, the site is the remnant of a once-extensive, apparently well-stratified and deep midden, located in a high-walled sea-washed shelter formed at the base of cliffs, beside broad rock platforms and a reliable source of water.

AIMS OF THE EXCAVATIONS

Specific Research

The more specific aspects of our research aims were closely related to earlier research by one of us on coastal exploitation patterns and adaptations (Vanderwal 1978, Vanderwal & Horton 1983). The Moonlight Head excavations also fitted into the development of knowledge of and research into the coastal archaeology of Victoria (Coutts 1981a, Coutts *et al.* 1976). This, combined with research on coastal sites elsewhere in Australia (e.g. see articles in Bowdler 1982), provides the possibility of assessing variations in the exploitation of coastal resources in different localities and situations. In this context the relatively unusual setting of Moonlight Head Rockshelter, its apparent depth, and its integrity as a closely defined stratified site, were seen to be of particular interest and value.

Salvage

As shown by the work of the Victoria Archaeological Survey, coastal middens are constantly being threatened by both natural and human activities (Coutts *et al.* 1976). They are certainly the most obviously threatened sites. This site was being eroded, and would not have survived in any reasonable form for very much longer.

Teaching

The project was envisaged as providing an opportunity for fieldwork for students. A further consideration was the acquisition of data which senior students could use as the basis for their own research projects. These aspects were all developed in the field, in laboratory sessions, and in the preparation of the final report.

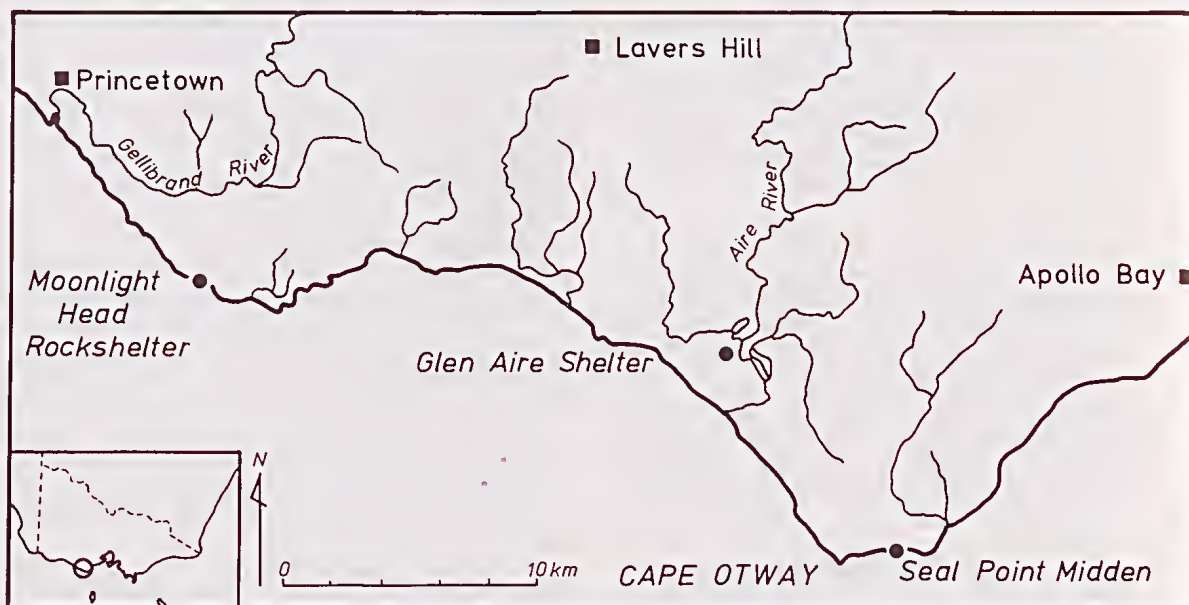


Fig. 1—Map showing localities mentioned in text.



Fig. 2—Coastal environment of the Moonlight Head Rockshelter. The site is in the middle distance.

Regional Research

At a more general level the Moonlight Head excavations were envisaged as providing a starting point for future research in the general area of the Gellibrand River. This study, now being carried out by one of us (DZ), will ultimately place this site in a regional context.

THE EXCAVATIONS

METHODS

General

The nature and location of the site posed some particular and unusual logistical problems. Access to the rockshelter, as already indicated, was difficult—but in addition the archaeological deposits were covered by massive blocks of sandstone. Extremely poor weather conditions added to an already arduous field situation: during the six weeks at the site there were not more than three days when it did not rain. Although it was mid-summer, it was windy and bitterly cold. Storms and the resulting high seas made access along the beaches (otherwise relatively easy) at first difficult, later dangerous, and finally impossible. The alternative route was hardly less hazardous. Equipment and finds had to be carried to and from the site over rough, steep terrain.

Organisation

The site was laid out in a metric grid, aligned with the nearby cliff wall, in order to take maximum advantage of the space cleared by the initial removal of overburden (see Figure 3 for the layout of the grid). For convenience of description a conventional 'north' is defined. This is in fact more correctly northeast. In discussion of the excavation units, however, this conventional 'north' is used unless otherwise indicated.

Units. Within this grid, six Units, of different size,

were excavated and materials from within each were kept together. Their size was dictated partly by the nature of the site, and partly by considerations of time. Two units were 1 m², three were 0.5 m², and one was 0.25 m², making a total area excavated of 3.75 m². These units were excavated independently, marking the relevant points on adjacent units to facilitate correlations.

Removal Numbers. Within each unit excavation proceeded by defined Removals. This neutral term covers any defined deposit—an arbitrary split, a stratigraphic layer or lens, or a feature (such as a hearth). An attempt was made, where at all feasible, to excavate by stratigraphic deposits, although the complex nature of the interleaved and minor mixed lenses of midden material made this difficult in practice. Some clearer lenses and layers, especially of sand or roof-fall, could, however, be traced across from one Unit to another.

Levels. Levels accurate to the nearest centimetre measured from a fixed datum were taken at the corners, centres of each side, and centre of the Unit after each Removal.

Sections. Before excavating the initially clear face of the midden, and after completion of each Unit, or set of Units, sections were drawn showing the major stratigraphic features and spot-heights of relevant removals. The final drawing of the north and east sections of Unit 106 (the clearest and deepest section) could not be completed as the wall collapsed under a massive rock fall.

Recording. Standard procedures were followed, recording the nature of each Removal, including Munsell colours (duplicate readings), and pH values for all Removals in Unit 41. About 90 minutes of Super-8 movie film were shot, to provide a more dynamic record

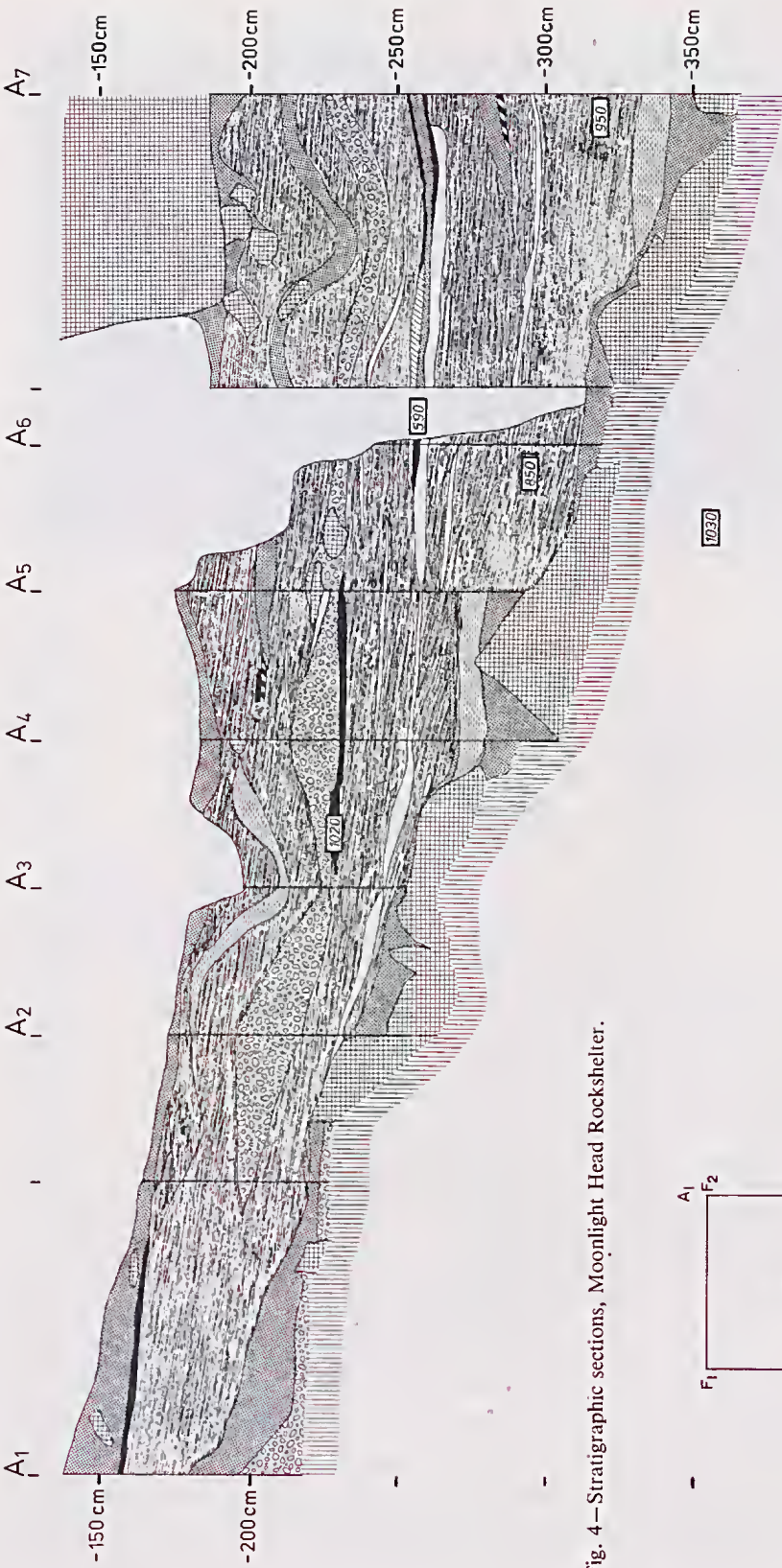


Fig. 4—Stratigraphic sections, Moonlight Head Rockshelter.

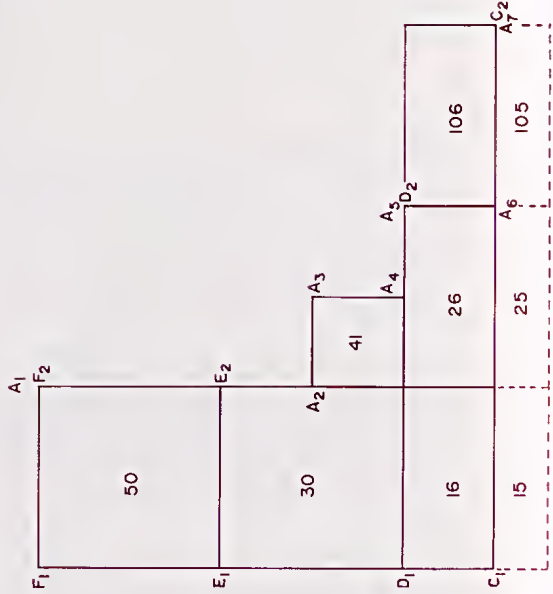


Fig. 3—Plan of excavation at the Moonlight Head Rockshelter. Subscripted letters refer to stratigraphic section drawings (Figs 4, 5). Orientation is conventional north.

MOONLIGHT HEAD ROCKSHELTER

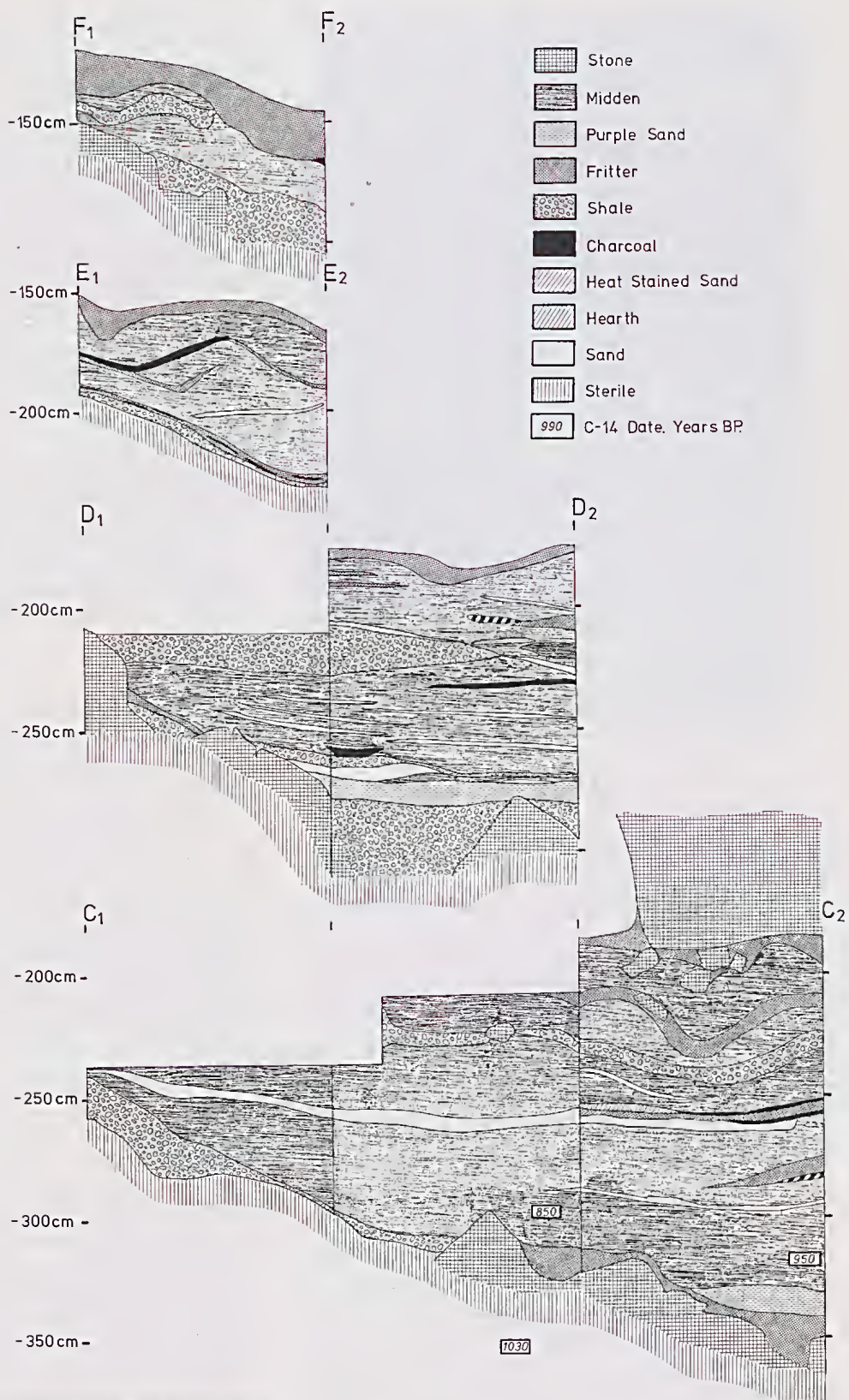


Fig. 5—Stratigraphic sections, Moonlight Head Rockshelter.



Fig. 6—Stratigraphic section of Unit 106, Moonlight Head Rockshelter.

of the excavations, with potential for producing a film on excavation methods.

Collection and Sieving. All deposits excavated were processed in nested sieves of 12, 6 and 3 mm ($\phi = -6.2, -3.2$ and -1.2). Stone artefacts and bones were separated and marked individually with Unit and Removal numbers. All shells were sorted by species, counted, and weighed to the nearest gram. Shells from most units were discarded after processing, although all those from Unit 106 were retained for more detailed analysis. Samples of soil, and of carbon for dating, were taken as required. All sieve residues and other material from Unit 106 were retained, and are available for further analysis.

PROCESS OF EXCAVATION

The heavy blocks on top of the deposits were broken up by hammer and chisel, and levered or winched away. Some 5 tonnes of rock were removed in this way, exposing a khaki sandstone grit layer which may have weathered off the roof immediately prior to the massive roof-fall, or off the fallen blocks themselves.

We were then able to take advantage of the vertical (SW) face of the site to work into it from the side—that is, to see layering in section and then attempt to trace

these often fugitive lenses in plan as each was removed. The same process of working on units after examination of both exposed horizontal and visible vertical aspects was applied in all cases.

The originally exposed face of the site (running across the centre of grid squares 1, 2 and 10) sloped outward toward its base. After preliminary cleaning, excavation began in Units 16 and 26 (the northern halves of squares 1 and 2). The shape of the eroded face of these units limited excavation to the lower sections: the upper deposits, seen in sections, were not excavated in the squares themselves. This exposed the vertical face of squares 3 and 4; square 3 was excavated as a square metre Unit (Unit 30). The next square to the North, 5, was then excavated, again as a full square metre (Unit 50). These two Units were relatively shallow, with the midden deposits thinning out as the underlying rock sloped up towards the back of the shelter.

Pressure of time, and of overburden, restricted excavation in square 4 to a quarter (Unit 41). The final Unit excavated was the 0.5 square metre Unit 106. A massive block of sandstone on top of this Unit could not be removed without destroying the midden deposits, but the depth of this part of the site made its excavation desirable. This was only just achieved before the wall collapsed under the weight of the blocks.

STRATIGRAPHIC ANALYSIS

STRUCTURE OF THE SITE

As seen in the sections (Figs 4, 5, 6) deposits (especially to the north) tend to be horizontal, although bedrock (or sterile basal fall-and-fritter deposits) drops steeply away from the north to the south and from the west to the east.

The surface of the midden, below the major rock fall, tends to reflect the lie of the bedrock in the north-west while levelling off in the southern and eastern Units. The deposits are therefore shallower to the 'north' and 'west'. In some areas the horizontal bedding is disturbed—particularly in the 'south-eastern' Units (41, 106) where the massive impact of the final rock fall is clearly evident in the sections. Here the force and weight of the roof-fall has compressed deposits, and depressed parts of some layers by at least 20 cm.

ARCHAEOLOGICAL DEPOSITS

Several categories of deposit, for the most part horizontally bedded, may be defined.

Sandstone or shale roof-fall

a, heavy blocks (as on the surface of the site) or smaller chunks of rock represent major, or less dramatic, episodes of collapse from the cliff-wall or vault. b, khaki-brown grit or finer material, part of the constant frittering off the cliff, dusting the site, forming distinct deposits between episodes of midden formation.

Mixed midden lenses

Typical midden deposits form a complex interleaving of shell, burnt or heat-stained grit fritter, and charcoal mixed in with the sandstone grit matrix. For the most

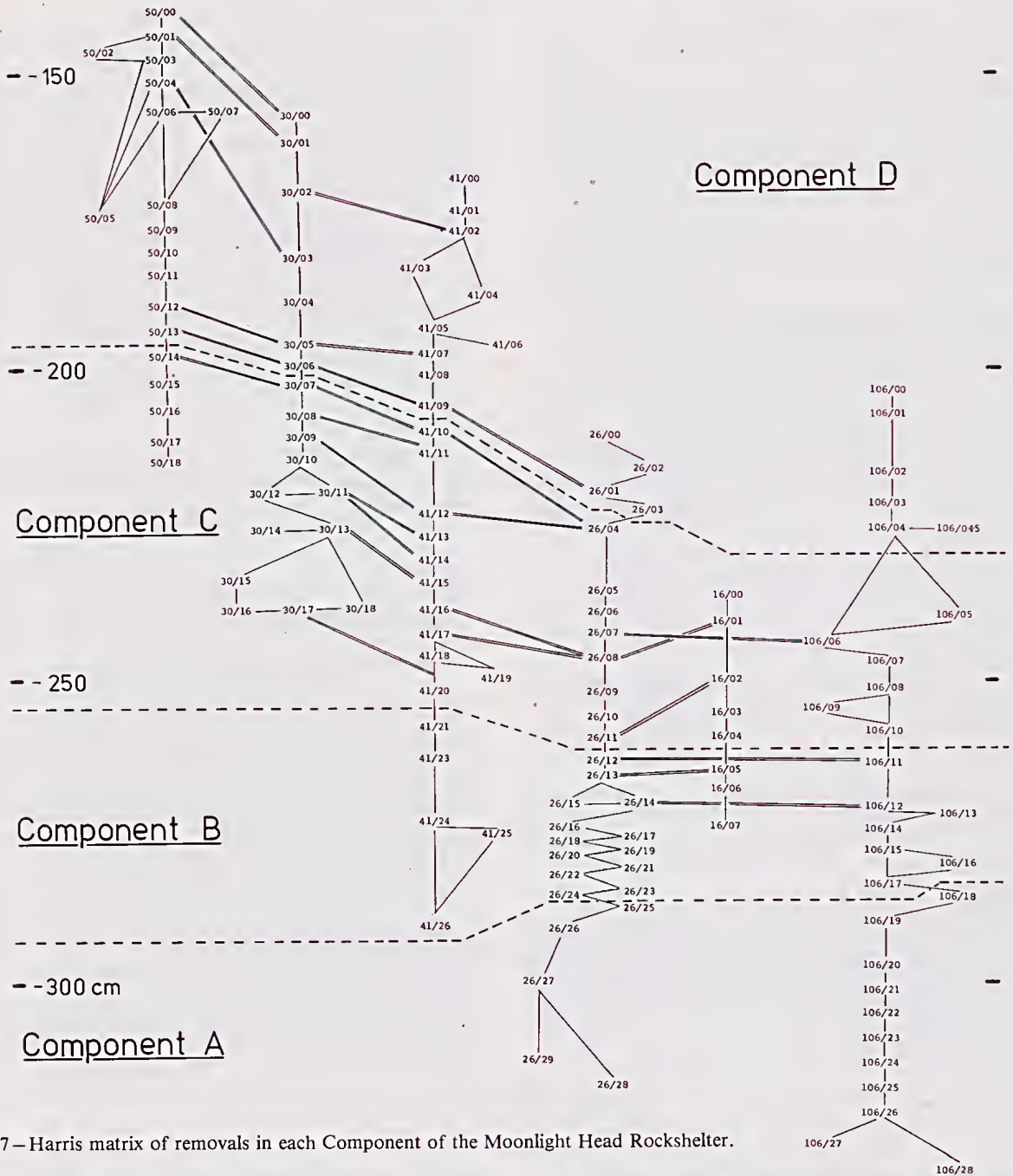


Fig. 7—Harris matrix of removals in each Component of the Moonlight Head Rockshelter.

part individual lenses could not be traced over more than small areas, often less than the area of any Unit.

Quartz sand

These sandy deposits, consisting of layered or lensed quartz beach sand, in some cases stained to a purple colour by fire, could have been brought to the site in a number of ways: a, carried in by people; b, blown in from sea-laid sand deposits in front of the site; c, washed in by exceptionally high tides; d, washed in from above.

In only one place do sandy deposits have any clear suggestion of having been water-laid, and even there the slight wave pattern could equally well have been caused by human or other natural factors. Wind, with some human transport into the site, would seem to be the most reasonable explanation for deposits, especially in the upper levels. Small rounded quartz grains were probably either washed in from above or derive from inclusions in the sandstone cliffs. The presence of a few patches of water-laid well-sorted clayey sediments also suggests water washing in from above. At the time that

TABLE 1
A, REMOVALS IN EACH COMPONENT

		Unit					
		50	30	16	41	26	106
C O M P O N E N T	D	0-13	0-6		0-9	0-3	0-4
	C	14-18	7-18	0-4	10-20	4-11	5-10
	B			5-7	21-26	12-24	11-17
	A					25-29	18-28

B, VOLUMES OF EACH COMPONENT IN EACH UNIT—
CUBIC METRES

		Unit						Total
		50	30	16	41	26	106	
	D	0.32	0.29		0.08	0.05	0.11	0.85
	C	0.23	0.30	0.09	0.11	0.14	0.11	0.98
	B			0.08	0.07	0.12	0.15	0.42
	A					0.16	0.19	0.35
Total		0.55	0.59	0.17	0.26	0.47	0.56	2.6

the shelter was occupied the rock and soil cover in the upper areas of the site would not have been present to prevent water from trickling into the shelter.

Charcoal

Some specific lenses of charcoal, as distinct from charcoal-rich midden deposits, could be defined. In some cases these underlie, or are associated with, 'hearth' features.

'Hearths'

These are interpreted from hard-packed circular orange (heat stained) gritty deposits, 1-3 cm thick in the centre and about 40 cm in diameter and generally associated with evidence of burning (heat-stained sand and charcoal).

MAJOR STRATIGRAPHIC COMPONENTS

The section drawings show the main stratigraphic features in the site, and the Harris Matrix demonstrates relationships between specific Removals (Figs 4, 5, 7).

Within each Unit the stratigraphic relationships are clear and straightforward. In considering the site as a whole, the complex layering of Removals, their unequal volumes and uneven surfaces make simple correlations between Units difficult. Some clear equivalences and easily recognised stratigraphic horizons can, however, be defined and traced across the site. These, together with equivalences between Removals in adjacent Units observed during excavation, make it possible to divide the site into 4 main stratigraphic Components.

Component A is found only in the deepest (southern) area of the site (Units 16, 106) and can be separated from later Removals by a distinct layer of quartz sand.

Component B above Component A, has as its upper limit a sandy and shale-and-sand layer that can be seen in section running (east-west) across Units 26, 41 and 106, again confirmed by correlations noted in the field.

Component C lies below a clear, well defined wedge of shale representing a fairly large fall from the western cliff wall.

Component D consists of the upper deposits in all units except 16.

The Removal numbers in each Component and their volumes are shown in Tables 1a and 1b.

While within each Unit the individual Removals are the minimum archaeologically defined units which may be used in relative sequence, these 4 main stratigraphic Components serve to link deposits from different Units and provide the possibility of broader-scale comparisons, and in that context form the 'finest reliable level of resolution' (Stern 1980: 76).

The volume of material in each Component, for each Unit, varies (Table 1b). In order to make valid comparisons appropriate compensation must be made. These are discussed in detail below.

The lower two Components (A and B) appeared during excavation to have a higher proportion of grit matrix to shell than other deposits. This cannot be due to

TABLE 2
MOONLIGHT HEAD RADIOCARBON DATES

Laboratory Code No.	Unit/removal	Date BP	Nature of Removal	Absolute level	Approx. cm below surface
GaK-9007	50/2	180 ± 90	burnt midden and charcoal concentration	146	6
GaK-9008	106/10	590 ± 110	dense charcoal in midden below hearth	261	41
GaK-9010	26/28	850 ± 110	mixed midden and roof fritter	298	87
Beta-1690	106/23	950 ± 65	midden and charcoal concentration	315	103
GaK-9009	41/13	1020 ± 110	midden lenses	231	51
GaK-9010	22/0	1030 ± 120	hearth	355	147

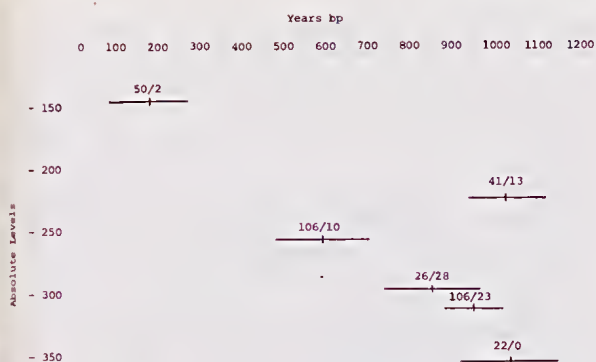


Fig. 8—Radiocarbon dated (C14) ranges of absolute levels (depth below datum) at the Moonlight Head Rockshelter.

differential preservation resulting from chemical decomposition, as all pH values recorded were the same (8 and 9). It must rather be related to a different depositional situation accentuated by the extremely irregular rocky basal surface.

REWORKING

Some questions have been raised at other Australian coastal sites about the possibilities of the reworking of deposits by the sea, while other disturbances of earlier deposits by subsequent occupation is a universal problem in archaeological sites. The features characteristic of reworked middens (Hughes & Sullivan 1974) cannot be demonstrated at the site and there is no reason to assume any significant disturbance by either natural or cultural agencies at Moonlight Head Rockshelter. Several additional factors which support this view of an absence of reworking by waves and the stratigraphic integrity of the site are: a, the presence of hearths throughout the deposits, from the earliest occupation; b, the horizontal bedding of features such as hearths; c, the abundance of charcoal, in the midden generally, and in association with hearths; d, no evidence of scouring by wave action; e, the violence of wave action on this high energy rocky coast would cause the removal of deposits at the front of the site rather than minor displacement; and f, additional support for the internal integrity of the stratigraphically defined Components was found during the analysis of the stone artefacts, as it proved possible

to refit some flint pieces from vertically non-adjacent Removals, but not between Components.

DATING

Six radiocarbon dates were obtained for deposits in the site (see Table 2). In all cases charcoal samples were collected with tweezers directly into aluminium foil. Sample GAK-9010 was collected from a hearth located during cleaning and preparation of the section, prior to the main excavation.

Dates are determined using the Libby half-life of 5568 (5570) years. Ranges are indicated at one standard deviation.

Five of these dates show a regular pattern of increasing age with depth (Figs 8, 9). Although direct correlation of depth (that is absolute depth) and age of deposits cannot be assumed with any midden site, particularly where the underlying basal material is as uneven as is the case at Moonlight Head, the consistent relationship observed here would seem to indicate a relatively even rate of accumulation of deposits in the site. Moreover the pattern could be taken to confirm our views on the integrity of the site, and the lack of significant reworking of the deposits by natural (or cultural) agencies.

The sixth date (Unit 41/13) is anomalous. In terms of absolute levels—height above bedrock or below the surface, or, more importantly, by natural stratigraphy—it is not possible to explain away this early date while the other 5 samples conform to a clear and predictable pattern. No other relevant carbon samples are available from Unit 41 to allow a check on contamination or other sources of error.

If we use only the five consistent dates, we may estimate the approximate ages of the four Components of the midden.

Component A—1000 BP to 800 BP

Component B—800 BP to 600 BP

Components C and D—600 BP to 200 BP

The apparently uniform rate of deposition, therefore, suggests that each of these Components was built up over a period of about 200 years.

Although the C14 dates can be used in this way to indicate a relatively constant rate of accumulation in the site, there are some important complicating factors. Of greatest significance is the increase in the density of cultural material in the upper Components. This was noted during excavation as a greater proportion of shell to sand matrix, and is confirmed by analysis of the shell counts in the lower deposits (see below).

A factor which mitigates the increase in shell density, but which cannot easily be measured, is the degree of compression of the deposits brought about by the initial impact, and subsequent pressure, of the massive blocks of roof-fall. A general impression of the force of this impact can be gained from the depressions seen clearly in the sections, particularly in Unit 106 (Figs 4, 5). The midden would have been higher (i.e. more loosely, less densely, structured) before the rock fall, which has compressed the deposits, reducing their volume, and so increasing the apparent density of cultural material. It is, nevertheless, clear that in the upper Components the in-

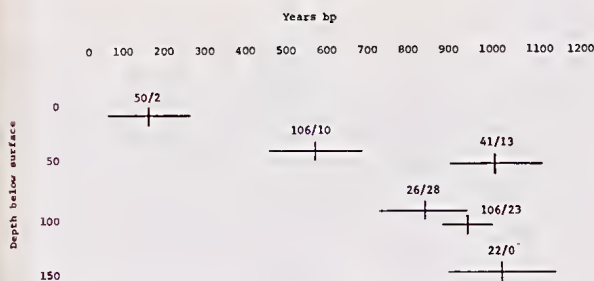


Fig. 9—Radiocarbon dated (C14) ranges of depth below surface at the Moonlight Head Rockshelter.

TABLE 3
FLINT CORES

Unit	Removal	Weight grams
30	04	150.7
30	05	33.4
30	12	32.0
50	15	16.6
50	15	17.7
106	10	35.2
106	12	125.4
Mean		58.7

crease in the relative quantity of shell is indicative of change in the nature of deposition. The greater proportion of sand relative to shell in the lower Components can be ascribed, in part, to the different catchment afforded to wind-blown sand by the jagged rocky base of the site, but may have been due to less intensive occupation—or usage—of the site, as suggested by the analysis.

Although it is impossible to assess, it may well be that the primary focus of occupation at the site in the earlier periods was away from the preserved (i.e. excavated) sections, so that the change in the observed pattern of accumulation was due not to any overall change in site usage, but to a shift of the focus of discard within the site as deposits built up.

While the greater density of shell in the upper Components could be ascribed to some internal change within the site, the fact that the same pattern is repeated in both stone and bone may support an interpretation of a general increase in the intensity of site usage. This problem is examined in greater detail below.

AREA II

One square metre was excavated on the small flat area near the waterfall above the main site.

A maximum of 50 cm of deposit was excavated, with rock appearing from 10 cm below the surface. An upper deposit of coarser dark sand about 5-7 cm thick overlay more clayey deposits.

A few pieces of stone were recovered, but no shell or bone. It is likely that any substantial cultural deposits that may once have been in this area have been eroded off the small platform and down the cliff into the sea.

ANALYSIS

THE DATA

All excavated material was analysed. As noted above, all the deposit from Unit 106 was retained for analysis under laboratory conditions. The bulk of the non-soil deposit consisted of shellfish remains, though stone and bone artefacts and animal bone refuse were also recovered. In analysing the debris we employ a method of density compensation which allows objective comparison of the four components. We deal firstly with the stone and bone artefacts in an attempt to define the

TABLE 4
FLINT—COMPARISON OF MOONLIGHT HEAD AND SEAL POINT

	Flakes	Fragment/ Core Fragment
Moonlight		
Head	22.9% (55)	66.3% (159)
Seal Point	85.5% (3592)	4.3% (181)
	(From Lourandos 1980: 253)	

technology of those who occupied Moonlight Head Rockshelter from time to time. This is followed by the shellfish analysis in which a diversity measure is developed for comparing collection strategies. Analysis of the other fauna completes our study of exploitation patterns, more fully developed below.

Density Compensation for Data Analysis

While it is legitimate to compare the various layers in a site in terms of the proportions that each category of material contributes to each deposit, considerable problems arise if the differences in absolute quantity are to be studied. A major problem arises when the excavated volumes of layers within the site are different, as is the case with MLH (see Table 1), and also if comparisons are to be made between sites. It is clearly not appropriate to compare the absolute quantities from different excavated volumes.

The basic method of compensation for different excavated volumes is to divide the quantity of the items under study by the volume of the deposit. This gives a standard figure for the density, or concentration. Bowdler (1979: 408), for example, uses this method for comparing density of fish at Cave Bay Cave and Rocky

TABLE 5
FLINT UTILISED PIECES

Unit	Removal	Weight grams	Cortex present	Flake = 1 Frag = 0
106	01	2.5	0	1
106	01	23.0	1	0
106	01	2.8	0	0
106	02	1.1	1	0
106	03	3.0	1	0
106	04	67.0	1	1
50	01	23.8	1	0
50	06	13.8	1	0
50	13	11.3	0	0
50	13	29.1	1	0
26	01	4.3	1	1
26	03	22.8	1	0
30	06	3.5	1	0
41	09	3.4	1	1
106	07	1.8	0	0
30	12	19.3	1	0
106	11	17.5	1	0
30	12	14.1	1	0
106	12	11.3	1	0

Cape. However, Vanderwal and Horton (1983) argue that this method is only appropriate when the depositional environment is similar. Thus, even intra-site comparisons may not be valid for a site deposited over several climatic phases, and the situation may be more complex than this.

Hughes and Lampert (1982) suggested positive correlation between the amount of sediment deposited and increased site usage, measured by the number of implements per unit time. This involves the construction of a depth/age curve for each site to show changing rates of sedimentation (Hughes & Djohadze 1980). While use of depth/age curves may avoid some problems associated with varied site densities, the margin for error in radiocarbon dates leaves some uncertainty. For many sites it is not possible to construct a depth/age curve, due to insufficient data. Furthermore, for inter-, or even in some cases intra-site comparisons, the different surface areas excavated must be taken into account in assessing any kind of absolute measure for the quantity of items deposited.

Comparison with other sites is often difficult where site reports do not give clear information, making it necessary to estimate volumes on the basis of section drawings and occasional details given in the text. The volumes of the deposits at MLH have been calculated directly from the level readings taken during excavation.

At MLH the locations of five dated radiocarbon samples suggest a decreasing rate of deposition. Although each Component covers approximately two hundred years, each is of different excavated area and volume. While the density of any material may be computed, interpretation is complicated by the presence of sandstone blocks in some deposits, and a varying amount of beach sand and other sediments.

In an attempt to lessen the bias of these factors, in each Component the density figures for stone artefacts and bone were adjusted in relation to the shell density, with the shell density held as a constant. In practice this was done by selecting Component D as the standard, dividing the shell density for this Component by that for each Component in turn, and multiplying the stone and bone densities by the resultant factor. In this way, change in bone and stone, relative to the shell, can be seen.

STONE ARTEFACTS

The relatively small sample of stone restricted its analysis to the quantification of the use of stone through time and its documentation for comparison with other assemblages. Small unflaked beach pebbles, roof-fall, stone collected from the surface and the MLH II excavation are excluded from the sample. The surface collection is not considered to provide sufficient control to be comparable with the excavated material, nor is it possible to relate the few flakes from MLH II to the time sequence of the main excavation.

The stone was analysed by Unit and individual Removal. Details of the latter provenance are available elsewhere (Zobel 1982: table 6).

Raw Material Types

The stone was first divided into three groups based on raw material. 1, flint includes all the flaked flint, varying in colour from light grey and light brown to almost black. The one unbroken pebble recovered is not included in the analysis. 2, quartz includes all quartz, which is also highly variable in colour. 3, all other worked stone, including sandstone, quartzite and beach pebbles of various colours.

Morphological Types of Flint

1, cores have signs of flake scars and negative bulbs of percussion, and are listed in Table 3. 2, flakes are characterised by one or more of a striking platform, hinge fracture or bulb of percussion. Not all flakes have the striking platform intact as these may either have been further modified after flaking, or disintegrated on impact. 3, fragments includes all pieces of flint which are neither flakes nor cores.

While at first sight the categories used by us may seem to be comparable to those used by Lourandos for the Seal Point assemblage, this is not the case. Lourandos (1980: 244), defined 'flakes' as: 'recognised by the bulb of percussion *and* by their conchoidal appearance' (emphasis added). Table 4 shows a comparison of the percentage frequency and number of 'flake' and 'fragment'/'core fragment' for Seal Point and MLH. Although Lourandos does not distinguish between raw materials, and it is unclear whether the retouched/ utilized pieces are also included in these overall morphological categories, the magnitude of the difference indicates a systematic variation in classification criteria. Lourandos (1980: 247) described his 'core fragments' as 'chunky, somewhat like cores themselves'. While our category of 'fragment' includes such items, it also includes a large number of small pieces, some weighing less than 1 gm. None bear evidence of the direct application of force; rather, they appear to be the result of 'shatter flaking' when the core is struck, as only one flake of several produced will show evidence of impact. Experiments with similar material indicate that this is a frequent occurrence (R. L. K. Fullagar pers. comm.).

Utilisation

The flint pieces in each of the three categories were examined for evidence of use. This was detected primarily by the presence of retouch and macroscopic edge fracturing, supplemented by microscopic examination. Table 5 lists the 19 pieces identified as utilised, indicating whether they are flakes or fragments (use was not detected on any of the cores), and whether or not cortex is present.

While one piece (from 106/02) shows evidence of having been used as a drill (R. L. K. Fullagar pers. comm.), a detailed use-wear analysis to determine the type of use was not undertaken for any other tools. Most wear, however, is consistent with woodworking (R. L. K. Fullagar pers. comm.).

The main areas of identifying the utilised pieces are: 1, to determine the proportion of 'used' to 'unused'

items. It is not clear that these data are comparable to those from other sites in the same way that morphological types are, for the application of use-wear studies is not uniform. For example, while 13.1% of flint pieces at Glen Aire II are identified as utilised (Fullagar 1982), only 7.9% were identified at MLH. The Glen Aire material has, however, undergone a much more detailed use-wear analysis which may account for the greater proportion of used pieces recognised at that site. 2, to discover criteria for selection of tools from the many flakes/fragments. 3, to determine whether or not tools were being manufactured at the site, and if their presence/absence correlates with any other factor.

Discussion

In reporting the Glen Aire excavation Mulvaney (1962) noted the lack of formal tools (after McCarthy 1976). Further research has indicated that this is a widespread phenomenon in recent Victorian prehistory (Coutts 1970, 1981a, 1981b, Coutts *et al.* 1976, Lourandos 1980, Wesson 1981, Fullagar 1982).

Coutts has proposed that the move away from formal tool types may have resulted from the need to conserve inland stone resources, formal tools being more wasteful to manufacture. He suggested this may be due

to increasing population, and stone resources coming under the control of smaller social groups. When this trend spread to the coast, where flint was abundant, a 'throw away' technology developed (Coutts 1981b).

No recognised morphological types have been identified among the MLH flint artefacts, nor is there much evidence of secondary working. Only 4 of the 19 utilised pieces are classified as flakes. The shapes are highly variable (see illustrations in Zobel 1982). The weights of the pieces range from 1.1 to 67.0 gm, with a mean of 14.5 gm and a high coefficient of variation (107%), indicating that the weights are highly dispersed about the mean.

It may be argued that pieces were not struck with an aim of producing a specific morphology. The lack of secondary working and the fact that many of the used pieces are fragments suggests that any piece with a suitable edge and convenient shape was selected for use. The general pattern of recent Victorian stone tool manufacture makes the alternative hypothesis that more formal tools were produced but did not find their way into the deposits, unlikely.

Change Through Time

The greatest change through the Components is the

TABLE 6
STONE ARTEFACTS

U N 1 T	C O M P.	Flint used		Cores		Flakes		Fragments		Quartz		Other	
		N	GM.	N	GM.	N	GM.	N	GM.	N	GM.	N	GM.
16	C							6	10.7			1	4.0
26	D	2	27.1					3	17.8	1	1.0	1	40.9
26	C					2	14.1	5	7.8	1	29.0	2	63.0
26	B					1	4.1	2	1.6	2	15.0	2	441.0
30	D	1	3.5	2	184.1	12	82.7	34	261.7	9	54.0	4	266.0
30	C	2	33.4	1	33.4	6	41.5	31	93.1	4	10.0	1	592.0
41	D	1	3.4			3	4.3	8	26.6	6	18.7	4	418.4
41	C					1	5.6	8	52.3	2	0.8	2	11.3
50	D	4	78.0			9	48.4	20	109.0	3	4.0	11	616.5
50	C			2	34.3	2	11.3	8	75.0			1	1.0
106	D	6	99.4			8	91.6	18	57.9	2	184.0	2	324.0
106	C	1	1.8	1	35.2	3	12.4	10	39.4				
106	B	2	28.8	1	125.4	8	19.5	5	4.3	3	442.0		
106	A							1	4.0				
S	D	14	211.4	2	184.1	32	350.1	83	473.0	21	257.7	22	1563.8
S	C	3	35.2	4	101.5	14	96.2	68	278.3	7	39.8	7	671.3
S	B	2	28.8	1	125.4	9	23.6	7	5.9	5	457.0	2	441.0
S	A							1	4.0				
Total		19	275.4	7	411.0	55	469.9	159	760.7	33	754.5	31	2671.1

S = All units combined into components

N = Number of items

GM = Weight of grouped items

TABLE 7
STONE DENSITY—BY NUMBER

		Flint	Quartz	Other
C				
O	D	154.1	24.7	25.4
M				
P	C	90.8	7.1	7.1
O				
N	B	45.2	11.9	4.8
E				
N	A	2.9	0.0	0.0
T				
Mean		73.3	14.6	12.4
S.D.		64.8	9.1	11.3
C.V.		88%	62.3%	90.7%

increase in the relative quantity of stone from the lower Components to the upper (Table 6). For the raw number of pieces this trend is evident in all categories, other than for cores. However, as each Component is of a different excavated volume, these numbers were converted to density measures. The results (Table 7) show that the trend is still clearly evident. Coefficients of variation were calculated to compare the degree of change for each type of raw material, to give some indication of the magnitude of the change. It can be seen that the change in flint and 'other' is similar, while quartz, a minimal element, is slightly more stable. The reason for this is unclear. The quartz pieces are rather large, with an average weight of 22.9 gm compared to 7.9 gm for flint.

Chi-square tests on the frequency of raw materials (Table 8) found in Components B, C and D indicate that no significant differences exist at the $p < 0.05$ level. Component A was not included because of inadequate sample size. Further tests between the numbers of flint cores, flakes and fragments (Table 9) show significant differences between Components D and C, and C and B (used and unused pieces are combined). Tests conducted on the proportions of used to unused flint pieces indicate no significant differences (Table 9).

The only difference seen, then, is one involving the ratios of flakes to fragments; this, and our knowledge of

TABLE 8
CONTINGENCY TABLE ANALYSIS: RAW MATERIAL BY NUMBER

Component	Flint	Quartz	Other
D	131	21	22
C	89	7	7
	Chi square = 4.90		df = 2
	p = 0.08		
Component	Flint	Quartz	Other
C	89	7	7
B	19	5	2
	Chi square = 3.92		df = 2
	p = 0.14		
	Yeats' correction is applied		

TABLE 9
CONTINGENCY TABLE ANALYSIS: FLINT MORPHOLOGY

Component	Cores	Flakes	Fragments
D	2	42	87
C	4	14	71
	Chi square = 8.58		df = 2
	p = 0.1		
	Yeats' correction is applied		
Component	Cores	Flakes	Fragments
C	4	14	71
B	1	9	9
	Chi square = 7.95		df = 2
	p = 0.02		
	Yeats' correction is applied		
Component	Used	Unused	
D	14	117	
C	3	86	
	Chi square = 3.02		df = 1
	p = 0.08		
	Yeats' correction is applied		
Component	Used	Unused	
C	3	86	
B	2	17	
	Chi square = 0.5		df = 1
	p = 0.54		
	Yeats' correction is applied		

the material, leads us to suggest that flaking in the later Components may be less controlled, and that further analysis in similar situations is warranted. It is recognised, however, that the observations may be nothing more than the result of a fortuitous distribution.

Summary

The most common stone material throughout the occupation of the site is flint. The only significant change detected is the lower number of fragments in the earlier Components. This may be due to more careful flaking of the raw material, but does not seem to have affected the utilised portion of the assemblage, with the relative frequencies of the utilized pieces remaining fairly low.

Flint pebbles, and pebbles similar to much of the material in the category 'other', may be collected from the small stony beach directly in front of the site (cf. Scott-Virtue 1982). The quartz flakes present in the site come from waterworn pebbles, and although none have been seen on the beach, this may be the source. These raw materials, then, need not have been deliberately brought to the site.

Our view of stone use at the site is of a fairly unchanging general technology. The raw material was probably picked up at the site, broken, and suitable pieces selected for the task immediately in mind.

BONE ARTEFACTS

Two bone points were found. One with clear use

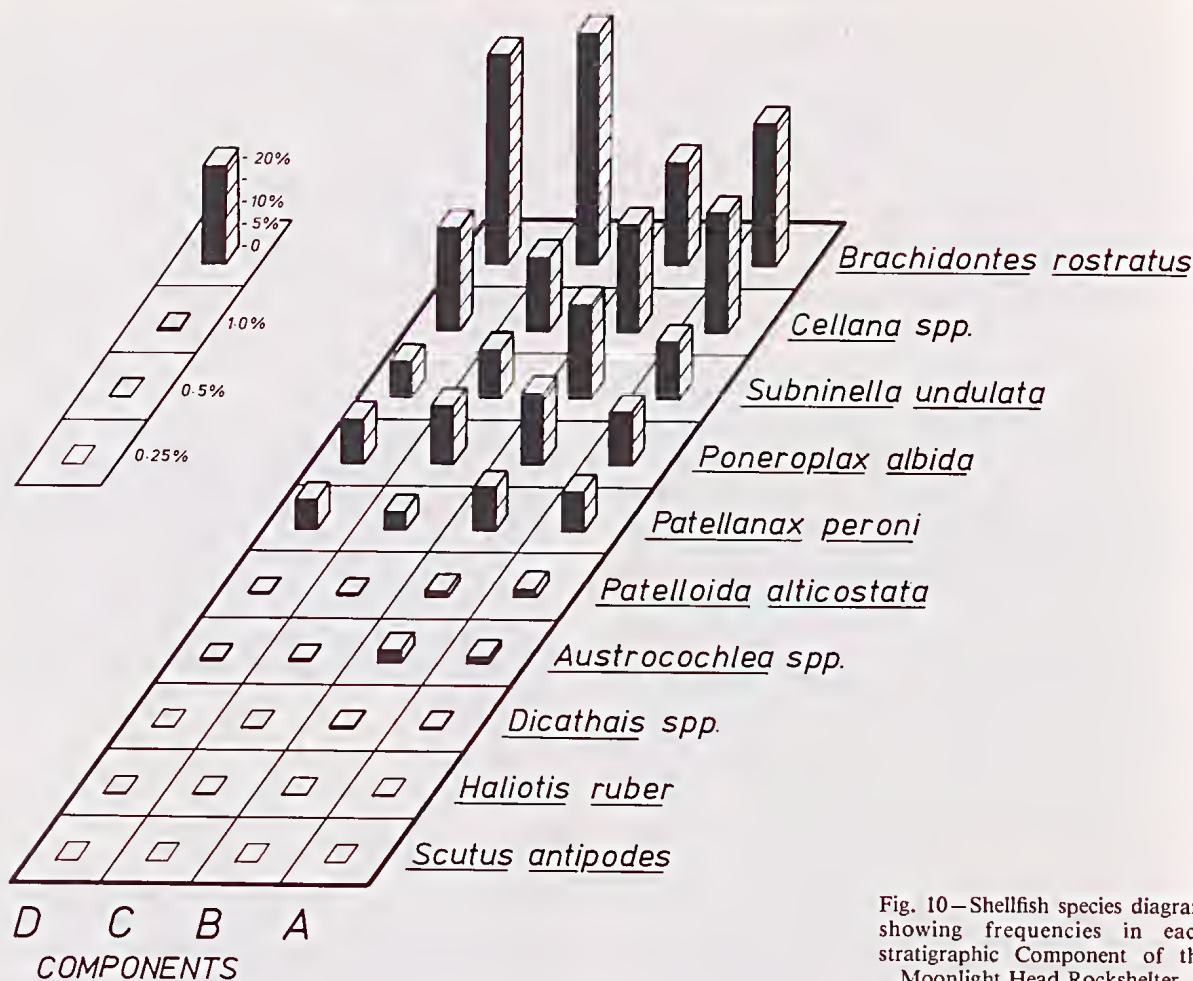


Fig. 10—Shellfish species diagram showing frequencies in each stratigraphic Component of the Moonlight Head Rockshelter.

wear, and breakage due to bending pressure, comes from Component C (Unit 26/11). This is approximately 80 mm long, and is formed on a macropod tibia. The other, which does not show clear evidence of use, may be termed a 'blank' (Fullagar 1982, Pickering 1979) and comes from Component A (Unit 106/02). This point, formed on a similar bone, includes the bone processes, and is approximately 60 mm long. Both would be classified as Unipoints according to Lampert's (1966) terminology, and Simple Unipoints in Pickering's (1979: 50).

MOLLUSCS

Species present in the midden

Ten species are considered to be of dietary importance (Table 10; Fig. 10).

Other species found in the midden were probably not eaten. Several varieties of *Siphonaria* are present in large numbers, but they are very small and would not provide much meat. It is suggested that they were probably collected incidentally, while gathering larger limpets. *Hipponix conicus*, present in very small numbers, is known

to live on larger shellfish (Macpherson & Gabriel 1962: 127), and was presumably collected along with their hosts. These species, together with some others found in small quantities, have not been included in the analysis (Zobel 1982).

The species which predominate in the deposits are *B. rostratus*, *Cellana* spp., *S. undulata* and *P. albida*. All 10 species, however, are present in each deposit except the volumetrically small 26/D; all the species are present in the adjoining deposits of the same Component, so their absence in 26/D is probably not significant.

Shellfish Ecology

Shellfish in the MLH midden were rock dwellers and can be found today on the rock platforms adjacent to the site. Factors related to the collection of shellfish are: 1, the intertidal zone each species inhabits; 2, abundance; 3, aggregation.

Following Bennett and Pope (1953: 107; 1960: 188-198) the intertidal fringe is divided into four zones.

supralittoral—above the high water mark.

littoral—within the mean tidal range.

TABLE 10
SHELLFISH RAW MNI PERCENTAGE FREQUENCIES AND CORRELATION COEFFICIENTS

SPECIES LIST

1 = <i>Haliotis ruber</i>	6 = <i>Patellanax peroni</i>
2 = <i>Scutis antipodes</i>	7 = <i>Patelloida alticostata</i>
3 = <i>Brachidontes rostratus</i>	8 = <i>Austrocochlea</i> sp.
4 = <i>Poneroplax albida</i>	9 = <i>Dicathais</i> sp.
5 = <i>Cellana</i> sp.	10 = <i>Subninella undulata</i>

PERCENTAGE FREQUENCIES OF MNI PER SPECIES—BY COMPONENTS

	1	2	3	4	5	6	7	8	9	10	
Component D	0.32	0.25	48.47	10.15	23.48	7.15	0.92	1.02	0.65	7.60	n = 44308
C	0.22	0.19	52.18	12.89	17.35	4.18	0.75	1.11	0.44	10.70	n = 31874
B	0.33	0.38	23.02	16.05	24.48	9.71	1.38	2.59	1.17	20.87	n = 9874
A	0.35	0.18	32.33	12.34	27.98	9.25	2.31	1.44	0.95	12.88	n = 10149
Mean	0.31	0.25	39.07	12.86	23.32	7.57	1.34	1.54	0.8	13.01	
S.D.	0.06	0.09	13.77	2.44	4.42	2.52	0.70	0.72	0.32	5.67	
C.V.%	19.0	36.8	35.25	18.9	18.97	33.3	52.19	46.94	40.15	43.56	

infralittoral—between the ranges of the low tide.

sublittoral—below the extreme low water mark.

Haliotis ruber (muttonfish or abalone) are the largest shellfish available on the rocky shore, are generally found between 1 and 10 m below the low water mark, and live in caves and crevices under the rock platform (Shepherd 1973: 222).

Scutis antipodes (duckbill) may be found in similar zones to *H. ruber*, but in relatively small quantities.

Brachidontes rostratus (beaked mussel) live in large, dense clusters. Bennett and Pope (1953: 118) counted as many as 2080 in one square foot. Observations at MLH indicate that large animals are rare, most being less than 25 mm long, and that this species prefers locations sheltered from the main wave action, yet with a constant trickle of water even at low tide.

Poneroplax albida (chiton) is found in the infralittoral zone, just above the low tide mark (MacPherson & Gabriel 1962). These animals are quite common, but are less densely aggregated than *Cellana* spp.

Cellana spp. has not been divided into species. Most are probably *C. tramoserica*, the most common littoral limpet found on the rock platform. The larger *Cellana solida* generally prefers more sheltered locations (King 1973: 145).

Patellanax peroni is much less common than *Cellana* in the mid-lower littoral zone.

Patelloida alticostata is not common, and is also found in the mid-lower littoral zone.

Austrocochlea spp. may be found throughout the littoral zone, but at present is rare at Moonlight Head.

Dicathais spp. is uncommon in the upper to sublittoral zones.

Subninella undulata is a common gastropod in the lower mid to sublittoral zones, and may be found in rock pools on the platform. Surveys conducted by Coutts (1976 *et al.*, appendix 3) indicate that individuals attain substantially greater sizes in the lower zones.

Physical Analysis

Excavated deposits were processed in the field, with the exception of those from Unit 106, reserved for laboratory processing. All material greater than 3 mm was analysed. Shell was sorted into species and then weighed to the nearest gram. It was possible to determine the species of a high proportion of the smaller fragments in the 3 mm fraction—data recorded under laboratory conditions from Unit 106 indicate that between 94% and 97% of the sample, by weight, was identified.

In addition, for Unit 106, three taxa, *Cellana* spp., *Brachidontes rostratus* and *Subninella undulata* were divided into four size classes. These are the major species in the shellfish component of the midden and each present different collecting situations. *B. rostratus* are found in large clusters of many hundreds, *Cellana* spp. are more dispersed and require more 'individual' collection, while most *S. undulata* live beneath the intertidal zone and must be dived for, although smaller animals may live nearer the surface.

Two common methods for quantifying faunal remains are 1, total weight per species, and 2, minimum numbers of individuals (MNI). Although the latter method may produce misleading results as the remains of a single animal may be spread through several stratigraphic samples (Grayson 1979: 203-224), shellfish remains are less susceptible to this problem than vertebrate fauna. Coleman (1966) considers that MNIs provide a better estimate of shellfish meat contribution.

Minimum numbers of individuals have been used in this study, and were determined as follows. Limpets with parts of the shell greater than one half are counted as one. *Brachidontes rostratus* were determined by dividing the total hinge count by two; and *Poneroplax albida* by dividing the total count of plates greater than one half by eight. Experiments in the field indicated that the extra time invested in separating the left and right

hinges, or the anterior valve of the chiton, would not yield significantly better results. *Dicathais* spp. and *Austrocochlea* spp. were determined using parts of the shell that had a substantial part of the spire and protoconch intact. While this procedure was carried out for *Subnirrella undulata*, more accurate figures were obtained from the opercula, which survive better than the rest of the shell, and these have been used in the analysis. *Haliotis ruber* are often highly fragmented, but determinations were made using parts having the central whorl, or the outer lip.

Meat Value Compensation

While meat weight may not be an accurate indicator of nutritional value (Shawcross 1967, Meehan 1977, 1982), it does provide a crude estimate of the food value of each species. The two main methods for calculating this are 1, by using a ratio of shell weight to meat weight (Bailey 1975, Anderson 1981: 111), or meat volume (Coutts *et al.* 1976: table 7); and 2, by estimating the average meat weight per animal for each species (Coleman 1966, Bowdler 1979: 216f, Luebbbers 1978: 250, Vanderwal & Horton 1983). We use a variation of the first method. Rather than using actual meat weights the MNIs for each species are multiplied by the following weighting factor. The factors are: *Subnirrella undulata*—2.7; *Haliotis ruber*—60.0; all other species—1.0. These factors have been derived from experimental work done on modern populations, and further modified after the size analysis of the archaeological samples was completed.

Diversity Measures

Diversity measures were calculated for each Component as a whole, to assess change in the pattern of shellfish use. The value of the measure rises as the proportions that the species contribute become more even. Thus, a (relatively) low measure indicates greater dependence on fewer resources. In this study base 10 logarithms have been used, and as ten species are always present—with the single exception of 26/D—the values for evenness will be identical to those for diversity.

There are two basic components of diversity measures; firstly, the number of species present, the *richness* or variety of the sample; and secondly, the *evenness*, that is the distribution of the individuals among the species (Odum 1971: 49). Several measures have been used by archaeologists, the major ones being 1, the Simpson index (Hardesty 1980), 2, the Shannon index (Yellen 1976, Coutts *et al.* 1976), and in the study of artefacts, 3, a geographer's measure (Whallon 1968, Frankel 1978). Vanderwal and Horton (1983) combine the use of the latter two. (See Zobel 1982, for formulae and further discussion).

In the treatment of data such as ours the Shannon index has been widely used and has thus received more attention from statisticians than the other formulae. Its behaviour is therefore better understood, and has been demonstrated to be evenly distributed for random samples (Odum 1971: 149). Diversity measures also retain information on the structure of the sample that is

lost by most other methods. It is possible to study many samples for general trends prior to undertaking a more sensitive analysis.

On raw MNI Component B has the highest diversity (Fig. 11), indicating that resource use is most even, with the trend of increasing dependence on fewer species in the later Components, C and D. Examination of Table 10 indicates that this may be attributed almost entirely to the increasing importance of *B. rostratus*. By comparison, the diversity for the MNIs weighted by meat value shows less variation (Fig. 11), indicating that the more intensively used species do not show an equivalent increase in meat weight contribution. This is because *B. rostratus* does not have a high weight/individual ratio compared to other species.

Correlations Between Species Collected

Table 10 includes the mean, standard deviation, and coefficient of variation for the frequencies of each species through the Components. Of the more common species, *S. undulata* shows the greatest variation, although this is still smaller than that of some of the rarer species. This variability can be further examined by considering the species in terms of the collecting situation they present to the prospective predator, described in section 4.2. To assess the relationship of changes in the quantities of one species with others, correlation coefficients were calculated on MNIs (Zobel 1982, table 4).

B. rostratus has a negative correlation with all the other species. The high negative correlation with *S. undulata* ($r = -0.89$) indicates that this is the major species being replaced. As reflected by the diversity measures, this represents a shift towards collecting a species with less meat per unit, but which is more easily collected.

The three species in the sublittoral zone show little correlation between the trends in their collection. Thus, it seems that there was no consistent attitude towards utilization of this zone; that is, it was species dependent

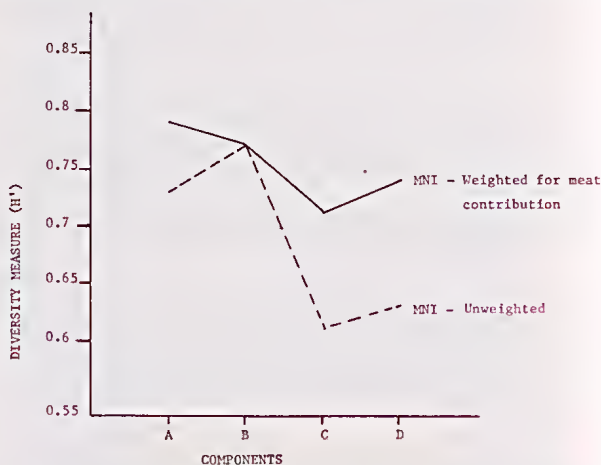


Fig. 11—Diversity (H) for unweighted and weighted minimum numbers of individuals (shellfish) in each Component of the Moonlight Head Rockshelter.

TABLE 11
SHELLFISH—MNI WEIGHTED FOR MEAT CONTRIBUTION PERCENTAGE FREQUENCIES AND CORRELATION COEFFICIENTS

SPECIES LIST

1 = <i>Haliotis ruber</i>	6 = <i>Patellanax peroni</i>
2 = <i>Scutus antipodes</i>	7 = <i>Patelloida alticostata</i>
3 = <i>Brachidontes rostratus</i>	8 = <i>Austrocochlea</i> sp.
4 = <i>Poneroplax albida</i>	9 = <i>Dicathais</i> sp.
5 = <i>Cellana</i> sp.	10 = <i>Suibninella undulata</i>

PERCENTAGE FREQUENCIES OF WEIGHTED MNI PER SPECIES—BY COMPONENTS

	1	2	3	4	5	6	7	8	9	10	
Component D	14.60	0.19	36.76	7.70	17.81	5.42	0.70	0.77	0.49	15.56	n = 58410
C	10.09	0.14	40.55	10.02	13.49	3.25	0.58	0.86	0.34	20.67	n = 41013
B	12.92	0.25	14.83	10.34	15.71	6.26	0.89	1.67	0.76	36.31	n = 15325
A	14.90	0.12	22.40	8.64	19.59	6.48	1.61	1.01	0.66	24.35	n = 14501
Mean	13.13	0.18	29.95	9.18	16.49	5.35	0.95	1.08	0.56	24.22	
S.D.	2.20	0.06	13.81	1.23	2.56	1.47	0.46	0.41	0.19	8.83	
C.V.%	16.79	33.16	46.10	13.40	15.54	27.54	48.82	37.79	32.98	36.44	

rather than zone dependent. Potentially, this zone could be the greatest source of shellfish meat. *H. ruber* and *S. undulata* have the largest quantity of meat per individual; the latter, particularly, is plentiful below the low tide mark.

Of the mid-littoral species, *Cellana* spp. shows a high correlation with *P. peroni* ($r=0.91$) and *P. alticostata* ($r=0.86$). These three are the only large limpets available, and may be found together. The correlation indicates that these were exploited as a group and little distinction was drawn between them.

In terms of shell numbers weighted for meat value (Table 11), basic relationships show a similar pattern but some differences are worth noting. The negative correlation of *B. rostratus* with *H. ruber* is less, as is the negative correlation of the mussel with *Cellana* spp. This emphasises the fact that it is *B. rostratus* which principally replaces *S. undulata*. The correlations between the sublittoral species, *H. ruber*, *S. antipodes*, and *S. undulata*, are close to zero, providing more evidence that the species within this zone were not exploited as a group. In contrast, the coefficients of correlation between the limpets remain relatively high (see Zobel 1982: table 5).

The coefficient of variation for *H. ruber* is less for meat values than for MNIs, indicating that as one of the important food-contributing shellfish, it is exploited at an even level throughout the occupation of the site. The same is also true for *Cellana* spp., although the other major species (*S. undulata* and *B. rostratus*) continue to show a relatively high variation.

Size Analysis (Fig. 12; Table 12)

B. rostratus, *Cellana* spp., and *S. undulata* were selected for size analysis. This was undertaken only for Unit 106, which spans all four Components and has approximately equal volumes in each Component.

Data on the size frequencies of modern populations were collected from several sources. For *S. undulata*, data are available from near Port Fairy, west of MLH

(Coutts *et al.* 1976: appendix 3); a collection was also made at MLH. Data on *Cellana tramoserica* are presented in Coutts (1970a, fig. 25) for several points on the Victorian coast. Data on *B. rostratus* and *Cellana* spp. were collected at MLH.

Brachidontes rostratus

Of the three species, *B. rostratus* has the greatest variation, mainly in the smaller size ranges (Fig. 12). While one must be cautious in correlating a reduction in the size range of a species with the level of predation (Swadling 1976), no clear pattern is evident. The upper Components, C and D, in which this species is the most frequent, do show quite different patterns of size class frequency. This may suggest that, when compared to other species, *B. rostratus* was more intensively collected, though the absolute level of intensity may not have increased.

This species lives in large clusters, and small clusters of larger individuals can be found amongst the mass of smaller individuals. While the age structure has not been assessed in detail, the distribution reflects a situation where few individuals reach a mature age (Fig. 13). The archaeological samples generally show a greater proportion of the slightly larger individuals. The most likely explanation for this seems to be that the species was collected by scraping clusters from the rocks, but that the

TABLE 12
SIZE CLASS RANGES FOR SHELLFISH

	Size Classes			
	1	2	3	4
<i>Cellana</i> spp.	0-25	25-35	35-45	45+
	Size class by length in mm			
<i>B. rostratus</i>	0-20	20-30	30-40	40+
	Size class by length in mm.			
<i>S. undulata</i>	0-2	2-3	3-4	4+
	Size class by weight of opercula in grams.			

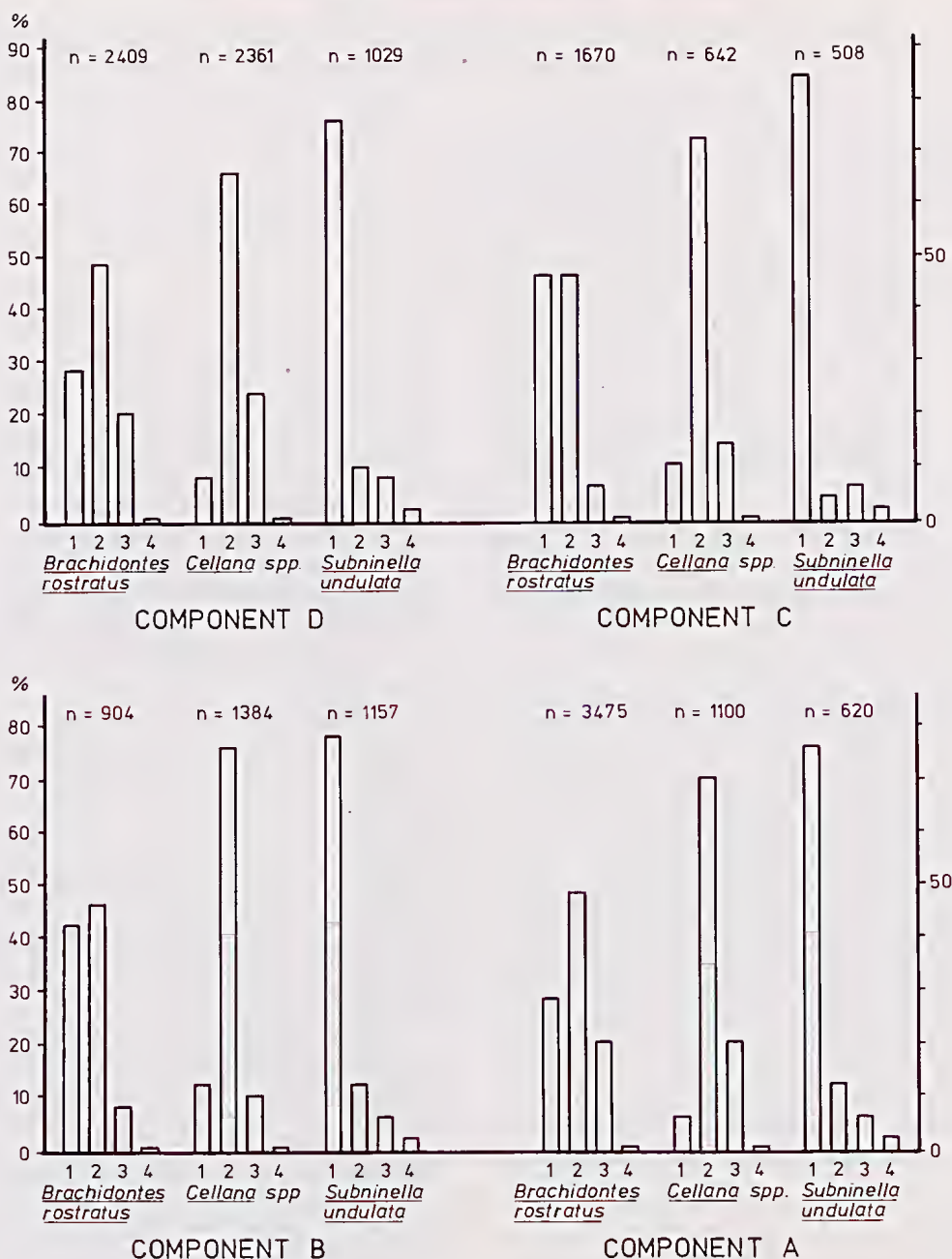


Fig. 12—Frequency bar graphs for shellfish species in each Component of the Moonlight Head Rockshelter.

areas collected from were selected because they included clusters of large shells, and that areas containing mostly small individuals were ignored. There seems, however, to have been no attempt made to select out smaller shells in areas from which collections were made.

Cellana spp.

Unlike *B. rostratus*, limpets require a more individual collection technique, allowing a greater degree

of selection. The size frequencies show a similar pattern in all Components, though the percentage in Class 3 fluctuates between 10% and 24%. As with *B. rostratus*, the size changes do not correlate with the change in proportions that the species contribute to the Components, once again perhaps indicating that the absolute intensity of exploitation did not change.

Figure 13 shows the size frequencies for two modern populations of *Cellana*, one from the Yanakie Peninsula

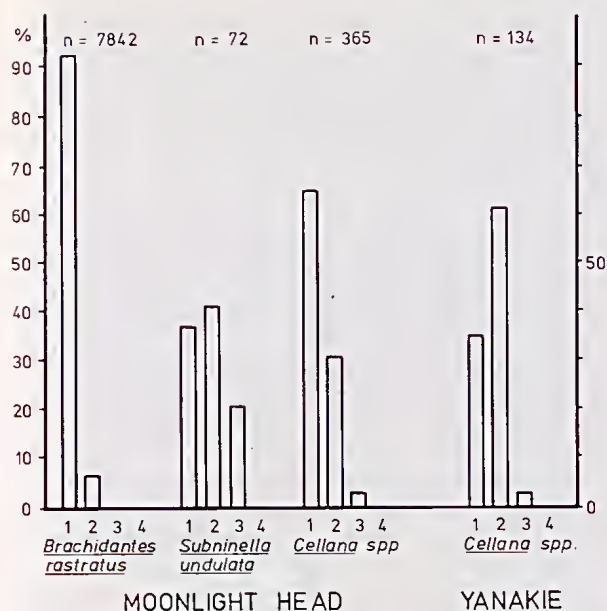


Fig. 13—Frequency bar graphs for shellfish species at the Moonlight Head Rockshelter and Yanakie sites.

(Coutts 1970a: fig. 25), the other from MLH. The Yanakie sample includes a greater number of the larger individuals, probably due to various ecological factors, including the greater intertidal range in that area.

Coutts (1970a: 65) concluded that some size selection towards collecting larger individuals was probably in evidence at the middens he investigated. The same appears to be the case at MLH, with the smaller individuals being ignored. Neither modern sample includes any individual of size Class Four although they are a consistent—if minor—component of the archaeological samples. Observations indicate that the rock platform at MLH supports large individuals in isolation, often quite removed from the areas more densely populated with smaller individuals.

Subninella undulata

Data presented by Coutts *et al.* (1976, appendix 3, fig. 38) indicate that smaller individuals are to be found in the shallow rock pools on the platforms, while larger ones are found mainly in deeper rock pools and crevices under the platform, so that smaller ones could be more easily exploited. The modern MLH sample was collected from the deeper regions, indicating that the larger animals are available in the area.

The frequencies for the archaeological sample of this species show the least variation through the Components, with the smaller individuals being dominant throughout. When this trend is compared with that for the modern sample collected at MLH (Fig. 13), it is clear that the larger individuals were either not available, or were not collected. If the larger *Subninella* were present during the past 1000 years in the same quantity as at present then they would have constituted an extensive potential resource. This species is not the major compo-

nent of the shell sample in the midden and it would seem that deep water stocks were not heavily exploited.

Shellfish Discussion and Summary

There seems to be no clear trend of size range fluctuation correlating with the changing trends of dependence on the different species. Over-exploitation—as evidenced by a reduction in the size ranges—is not likely to be a factor at MLH.

In looking at collecting strategies it is useful to distinguish two collecting zones—above and below the low water mark. In the upper zone the major species are the limpets (*Cellana* spp. and *P. peroni*), and the mussel (*B. rostratus*). The species present in this zone are exploited approximately in the proportions that they are available on the platform: thus the strategy is fine grained.

Exploitation of the subtidal zone, which could supply not only the greatest quantity, but also the most sustained meat yield, is not as extensive as might be expected. Sustained diving efforts were not made to collect the larger *H. ruber* and *S. undulata*.

Anderson (1981) has postulated a model for shellfish collecting strategies in which the collectors are assumed to take account of only the size of the individual animal, regardless of species. His model proposes that initial exploitation of the resource should be fine grained, but become more coarse grained, concentrating on the more abundant species as the larger animals from the other species are thinned out. While the diversity measures indicate a trend towards a coarse grained strategy of increasing reliance on *B. rostratus*, Anderson's model does not seem to adequately explain this, as another abundant species, *S. undulata*, was ignored. The exploitation pattern of the upper zone remains fairly fine grained.

This leads to the conclusion that shellfish were not a major contributor to the diet. Little evidence for a change in the intensity of exploitation of molluscs has been found. Furthermore, the decrease in exploitation of the sublittoral zone indicates that in a changing resource use schedule, shellfish were replaced by some more favoured resource.

OTHER FAUNA

Quantification

The bone in the site is considered to be the result of

TABLE 13
VERTEBRATE FAUNA MNI

	Total	Component			
		D	C	B	A
Labrid fish	13	4	7	1	1
Crayfish	10	6	1	1	2
Possum	7	4	3	—	—
Wallaby	2	2	—	—	—
Seal	2	—	1	—	1
Total	34	16	12	2	3

TABLE 14
BONE WEIGHT—WITHOUT SEAL

		Unit	16	26	30	41	50	106	Total
C O M P O N E N T	D		3.5	151.2	36.2	61.6	44.4		296.9
	C		10.6	26.8	62.9	10.1	9.7	14.5	134.9
	B		1.3	15.5		0.2		15.7	32.7
	A			2.7				23.0	25.7
									490.2
BONE WEIGHT—WITH SEAL IN GRAMS									
	D		3.5	152.2	36.2	61.6	44.4		296.9
	C		10.6	30.6	94.4	10.1	86.6	14.5	246.6
	B		1.3	15.5		0.2		15.7	32.7
	A			13.6				23.0	36.6
									612.8

human discard as there is no evidence of burrows or any other use of the site by animals, while in more recent times the midden was sealed by rock fall.

Quantification is by MNIs and by weight. MNIs are determined using principally the mandible, maxilla and teeth. Fish were analysed on the dentary and pharyngeal bones, and seal using vertebrae as this was all that was found in Component C, and a maxilla in Component A (Table 13). The bone, sorted only into seal/non-seal, was also weighed. This separation was made so that the greater mass of the seal bone would not mask changes among smaller species.

The amount of bone increases markedly from the lower level to the top of the site (Table 14), whether measured by MNI or by weight. Very high values of correlation between MNI and weight, including ($r=0.97$) and excluding ($r=0.99$) seal (Zobel 1982, table 16) indicate that both methods are providing much the same information. Unfortunately the number of cases is too small for tests of statistical significance to be applied.

In order to examine the relative change of the amount of bone through time the raw bone weights were converted into standard density measures by dividing by the volume of the appropriate deposit. Although somewhat reduced, the density measures still show a strong directional trend toward more bone in the upper deposits (see Zobel 1982, table 17). It is unlikely that any differences are due to varied preservation, as the pH readings at MLH are fairly constant, varying only between 8 and 9. Furthermore, the presence of large quantities of shell leads to more rapid mitigation of the chemical weathering effects of percolating water. The MLH deposit would probably have remained moist at all times due to its close proximity to the sea.

Analysis

The most common animal found at the site is parrot

fish (Labridae), followed by crayfish (*Jasus* sp.). Both are found through all Components, but are more common in the upper ones (Table 13). Land mammals, which were not determined in the lower Components, become increasingly important in the upper part of the site.

Fish and Crayfish

Parrot fish are most commonly found in rocky shore environments, and are generally considered the easiest fish to catch (Leach & Anderson 1979: 9, Bowdler & Lourandos 1982: 129, Jones 1978: 27, 32), although Leach and Anderson (1979: 4) consider them easier to catch in nets than with hooks. The most commonly surviving cranial bone of these fish at MLH is the inferior pharyngeal (which has also been noted in New Zealand sites, Leach and Anderson 1979: 6). The maximum length of these was measured on all but one, which was too fragmented (Fig. 14). If this distribution is compared to that of Seal Point (Bowdler & Lourandos 1982, fig. 3), it can be seen that the MLH sample shows a similar peak at around 20-25 mm, but has a narrower range. On the basis of their size analysis Bowdler and Lourandos (1982: 130) argued for fishing with fixed gill nets. They further argued for a correlation between bone point and fish frequencies (1982: 124). The presence of two bone points at MLH cannot be taken as evidence for either extensive manufacture or use.

The presence of parrot fish and crayfish through all Components, in conjunction with the shellfish, indicates a continuing use of the rock platform environment as an important source of food.

Seals

Two seals have been identified at MLH, one in Component A where a maxilla is present, the other in Component C, represented by several vertebrae. A seal may provide a considerable quantity of meat, but in terms of the overall use of the site, these individuals represent only two visits during one thousand years. The nearest seal colonies today are further west along the coast, on the offshore islands near Port Fairy (Ride 1970: 198). Though studies have indicated that seals are often washed up along the Victorian coast (Warneke 1975),

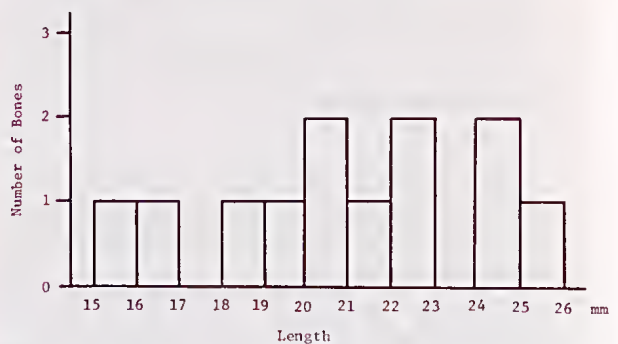


Fig. 14—Lengths of animal bones at the Moonlight Head Rockshelter.

their presence at MLH probably indicates opportunistic finds when people were in the area at the right moment.

Land Mammals

By far the most common land mammal represented at the site is the Common Ringtail Possum (*Pseudocheirus peregrinus*). This species is at present common and widespread in the Otway Ranges, preferring the coastal messmate forest environment (V.L.C.C. 1976: 292) or nesting in coastal tea-tree scrub (Ride 1970: 72).

Two wallaby-sized animals are present in Component D. The maxillae by which they were identified are fragmented, making positive identification difficult. With the exception of the bone point, remains of the larger macropods appear to be absent. Strictly adhering to methods of analysis developed in greater detail by Zobel (1982), we may note that, in terms of MNIs, land mammals are absent in the lower two Components. There seems to be no reason to believe that any major vegetational changes have taken place in the Otway region during the last thousand years (Head & Stuart 1980: 67). As it seems unlikely that the availability of land mammals has changed during the occupation of the site, a change in the nature of use of the site may be indicated.

Summary

While numbers of individuals are too small for statistical methods to be applied, two main trends in the non-molluscan faunal remains may be seen.

The quantity of bone by weight, compensated for density, shows a clear increase through time at the site, both in absolute terms and relative to the shell density. This is accounted for by an increase in fish, crayfish, and land mammals in the upper two Components.

Lourandos suggested that land mammals represented at Seal Point were isolated finds (1980: 291), in contrast to the marine resources, where the parrot fish, crabs, and some shellfish were found in the same ecological zone. In her interpretation of the Stockyard site, O'Connor (1980: 111) suggested that small land animals may have been collected by women on their way to the site. This may well be the case at MLH, as any route to the site passes through habitats suitable for the species present. The increase in these animals may still, however, indicate some decision to pay more attention to these resources during the latter period of occupation.

CONCLUSIONS

SITE FORMATION

The radiocarbon dates show a clear pattern in the depth/age diagrams (Figs 8, 9) with the possibility of a slightly slower rate of deposition in the upper half of the site. However, as the figures for shell density show (Table 15), Component D has nearly twice the density of the other Components. This is probably the result of compression of the upper layers by the extensive roof-fall. The rate of deposition can therefore be regarded as relatively constant.

To compensate for the effect of this compacting, and to examine the change in stone and bone relative to each other, and to shell, the density measures for the former two were adjusted to a constant shell density. As can be seen in Table 15, the weight of bone increases upward through the Components. The stone artefact quantities also increase, though this is not so marked in the upper three Components.

RESOURCE-USE

Change in resource-use may be explained in a variety of ways, including cultural and environmental explanations. A slight shift away from a marine-oriented economy may be seen at MLH, with a trend towards a more general exploitation of the area with a greater variety of resources being exploited. Different strategies in resource collection are in evidence, indicating a change in the logistical structure of settlement and exploitation.

While more of the time spent at the site was put into fishing for labrids in the later periods, less time was invested in shellfishing by concentrating on the more easily collected mussel (*B. rostratus*).

This increase in the use of land mammals is also seen at Seal Point, with the same species—the Common Ringtailed Possum—being by far the most frequently represented animal. Labrids are similarly the dominant fish species (Lourandos 1980). In his most recent discussion of Seal Point, Lourandos proposes that the increase of land fauna use reflects an increased availability of these resources (Bowdler & Lourandos 1982: 129). However, as no major vegetational changes occurred during the period of occupation of either site, no major fluctuations of resource availability need be assumed. A degree of circularity of argument is implied if simple frequencies of animals in a site are taken as an indicator of

TABLE 15
DENSITY OF BONE, STONE AND SHELL

		Shell MNI		Stone No.		Bone no seal grams		Bone with seal grams	
		X	Y	X	Y	X	Y	X	Y
Component	D	52121.1	1	207.1	207.1	349.3	349.3	349.3	349.3
Component	C	32524.5	1	106.1	170.0	134.4	215.4	251.6	403.2
Component	B	23509.5	1	61.9	137.2	77.9	172.7	77.9	172.7
Component	A	28997.1	1	20.0	35.9	73.4	131.2	104.6	188.0

X = Raw density measure

Y = Density measure adjusted by shell density.

availability. Unfortunately, the sample at MLH is too small to allow any more sophisticated analyses of the fauna available, as in order to make some assessment of the resource abundance, some assessment of the sex/age structure of the population must be made.

At Bass Point, in N.S.W. near Sydney, Bowdler found a pattern of shellfish change similar to that seen at Moonlight Head, with a trend away from exploiting the sublittoral gastropod *Ninella torquata*, and towards greater use of the mussel *Mytilus edulis* (1976: 255). As at Moonlight Head, this results in less meat per animal collected. The change observed in the Bass Point fish remains seems to be one of change in emphasis between species, rather than a trend toward or away from a concentration on fewer species; the diversity measures (H') are 0.66 and 0.67 for the upper and lower middens respectively (data from Bowdler 1976, table 1). Bowdler interpreted this change in exploitation as due to a historical change in technology—the introduction of fish-hooks—affecting the food-providing role of women. Similarly, Smith (1977), in relation to changing technology, discusses the possibilities for different structures of the groups exploiting Devon Downs.

As neither of these environmental or historical/cultural models seems entirely adequate at Moonlight Head, some discussion of other factors relating to resource use may be of value.

RESOURCE 'PULL'

Both Wilmsen (1973) and Jochim (1976: chapter four) have given theoretical consideration to the effect of the density, size, and mobility of resources on the optimal settlement patterns for effective exploitation. Based upon a theoretical model, in which 'least cost' in terms of time and energy is postulated, Jochim proposes that site locations will be closest to less mobile, more dense and less clustered resources (1976: 60).

Clearly, shellfish fulfill all of these criteria, and should, according to this model, have considerable influence on site location. Shellfish, furthermore, are a reliable resource. If the culling rate is not so high as to deplete the reserves—and no evidence for this was found at MLH—then a trip to any rock platform will supply a meal.

During the early period at the site, shellfish provided just such a reliable, but short-term, resource. During the later period, the inclusion of land mammals and increased reliance on fish provided greater variety of food.

SITE USE

The resource-use at MLH can best be understood in a wider context of other Victorian sites.

Seal Point, located about 45 km east along the coast from MLH, has been interpreted as a base camp (Lourandos 1980, Bowdler & Lourandos 1982). The most striking difference from MLH is the much greater quantity of stone and mammal bone. As noted above, the same species predominate, with the exception of seal which is much more important at Seal Point. The area of the pits analysed—F, G, I, and J—is 4 m, compared to 3.75 m at MLH; estimates of the volume of these pits

from the sections and data given in the text (Lourandos 1980), indicate a volume of about 3.25 m³, compared to 2.6 at MLH. Both sides were occupied over the last thousand years. The greater density of stone and bone at Seal Point indicates greater use of the site. The interpretation of this site as a 'base camp' is made on several grounds, including the presence of depressions thought to be hut pits.

In contrast to the situation at MLH, *S. undulata* is the dominant shellfish species (Bowdler & Lourandos 1982). An explanation for this may lie in the apparent longer occupations of Seal Point. The species on the littoral zone of the rock platform would not survive such sustained exploitation as the extensive sublittoral supply of *S. undulata*.

Comparative information on some other Victorian coastal sites may be found in Coutts *et al.* (1976). The Gippsland site of Clinton Rocks, which has been termed a 'temporary' camp (Coutts 1981a: 76) is dominated in all layers by *B. rostratus*; no other shell species contributes more than 10% in any layer. The evenness measure is low, 0.32, indicating a much greater dependence on this single resource than is evident at most other sites. Two middens excavated in the Port Fairy area show different distributions. At the Reamur Rocks site *S. undulata* predominate, the evenness index in 0.63, compared to 0.77 at The Craigs, indicating a more even use of the species at the latter site. (The evenness indices are recalculated from data provided by Coutts *et al.* 1976). It is clear that change in the use of the various shellfish species, both between and within sites, is due not only to the shellfish habitats adjacent to the site, but also the way the site fits into the resource use cycle.

Coutts (1981a), distinguishing between temporary camps and base camps, suggested that the latter may be expected to contain evidence of stone tool manufacture, and a greater quantity of bone remains than the former. The distinction may not, however, be so clear. At many points along the west Victorian coast, apparently *in situ* thin shell lenses, often only a few centimetres thick, are being exposed by eroding dunes. No stratigraphic features are commonly found in these sites (Coutts *et al.* 1976: 9-10). They are presumably the result of less specific site placement considerations. On morphological grounds, deep, stratified sites such as MLH and Seal Point are quite different.

No clear change in the stone artefacts at MLH has been found. Although a detailed use-wear analysis was not undertaken, Richard Fullagar has suggested that some of the wear patterns are consistent with wood-working (pers. comm.). We may postulate that this is due to maintenance of the organic parts of an extractive tool-kit. At the very least, we can say that stone tool manufacture and use is in evidence at MLH, although perhaps not to such a great extent as at Aire Shelter II (Fullagar 1982) or Seal Point.

It may be suggested that the distinction between base camp and temporary camp is not as clear as has been thought. Considerable variability exists in the mor-

phology and contents of Victorian coastal sites, and this variability can be seen as a continuum in the range of site type from residential base camps, such as Seal Point, to the thin shell lenses, possibly the result of a single visit. In behavioural terms certain types of sites may be suggested. One type would be the 'dinnertime' camp defined by Meehan (1982) for the Anbarra. She notes that these sites may either have been used once, or visited many times. The type is defined on the contents of the site, reflecting only the collecting and cooking of shellfish.

At the other extreme, a 'base camp' should reflect a wider range of tasks, including manufacture of the extractive tool-kit, and exploitation of a wider range of foods used in subsistence. Aire Shelter II may be placed midway along this continuum. While this site shows a wide range of activities, each occupation may not have been as lengthy as in a base camp, such as Seal Point. Within this broader behavioural model of site usage we may suggest that the concentrated deep midden at MLH probably assumed its form as a result of the particular shape of the shelter acting as a catchment for debris, and providing a focus for activity over successive occupations not found at open sites, rather than directly reflecting intensive use of the site.

We can then see the logistics of the subsistence strategies as being organised on several levels. The change in the use of Moonlight Head may reflect a slight shift in this logistical pattern, moving away from a less intensively used dinnertime camp, and towards a camp involving a wider range of activities and foraging strategies.

ACKNOWLEDGEMENTS

We thank Alec Neave for bringing the site to our attention, and Peter Coutts and Denise Gaughwin for commenting on drafts of this paper. The text was typed by Leigh Hawking, and some of the figures prepared by Rudy Frank. The many others who assisted with excavation and analysis of this material are also thanked. The project was funded by a La Trobe University Humanities Research Grant.

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REDESCRIPTION OF *NOTOEDICEROS TASMANIENSIS* BOUSFIELD AND A NOTE ON THE SYNONYMY OF *WARREYUS* BARNARD & DRUMMOND WITH *EXOEDICEROIDES* BOUSFIELD (CRUSTACEA: AMPHIPODA: EXOEDICEROTIDAE)

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ABSTRACT: *Notoediceros tasmaniensis* Bousfield 1983 was described incorrectly, and a full new description is presented. The genus *Exoediceroides* Bousfield 1983 (March) must supersede *Warreyus* Barnard & Drummond 1983 (June). A new key is provided to the eight genera (including the two new ones) now comprising the Exoedicerotidae Barnard & Drummond 1982.

Certain features of *Notoediceros tasmaniensis* Bousfield 1983 were incorrectly described by that author, notably the significant third uropod. The illustrations of this appendage are, owing to their extremely small size, uninterpretable, but uropod 3 is described as being 'unequally biramous'—a condition judged by Bousfield to constitute one of three major distinguishing characters in the separation of *Notoediceros* from closely related genera. Uropod 3 is, in fact, uniramous.

Our description of this genus was ready for press when it was pre-empted by Bousfield's paper; but we present our full description to correct and elaborate the brief original.

Bousfield (1983) also pre-empted *Warreyus* Barnard & Drummond 1983 with *Exoediceroides*. The very small size of the figures and scant description of the type species are quite inadequate, however, to permit distinction to be made between the two known species of this genus, both described previously: *Oediceros latrans* Haswell 1879; and *Exoediceros maculosus* Sheard 1936 (see Barnard & Drummond 1983).

Our examination of the carcass of the holotype (deposited recently in the Museum of Victoria) indicates that *Exoediceroides maximus* Bousfield 1983 is a synonym of *Oediceros latrans* Haswell.

LEGENDS

Capital letters describe morphological parts; lower case letters to the left of capital letters denote specimens cited in figure captions; lower case letters to the right of capital letters or in the body of any drawing are cited in the following list: A, antenna; B, body; C, coxa; D, dactyl; F, accessory flagellum; G, gnathopod; H, head; I, inner plate or ramus; J, pleopod; L, labium; M, mandible; O, outer plate or ramus; P, pereopod; Q, cuticle; R, uropod; S, maxilliped; T, telson; U, prebuccal anterior; W, pleon; X, maxilla; Y, gill; Z, brood plate (oostegite); d, dorsal; e, enlargement of edge; o, opposite; r, right; s, setae removed.

SYSTEMATICS

Family EXOEDICEROTIDAE

DIAGNOSIS: Amphipoda like Oedicerotidae but apices of rami on uropods 1-2 spinose and eyes, when present, paired.

VALID GENERA WITH TYPE SPECIES: *Exoediceros* Stebbing 1899 (*Oediceros fossor* Stimpson 1856) (= *Oediceros arenicola* Haswell 1879), *Bathyporeiapus* Schellenberg 1931 (*B. magellanicus* Schellenberg 1931), *Exoediceropsis* Schellenberg 1931 (*E. chiltoni* Schellenberg 1931), *Metoediceros* Schellenberg 1931 (*M. fuegiensis* Schellenberg 1931), *Parhalimедon* Chevreux 1906 (*P. turqueti* Chevreux 1906), *Patuki* Cooper & Fincham 1974 (*P. breviuropodus* Cooper & Fincham 1974), *Exoediceroides* Bousfield 1983 (*E. maximus* Bousfield 1983 = *Oediceros latrans* Haswell 1879), *Notoediceros* Bousfield 1983 (*N. tasmaniensis* Bousfield 1983).

OTHER SPECIES: *Bathyporeiapus bisetosus* Escofet 1970, *B. ruffoi* Escofet 1971, *Parhalimедon tropicalis* Barnard 1961, *Exoediceroides maculosus* (Sheard 1936), *Patuki roperi* Fenwick 1983.

KEY 1 TO THE GENERA

1. Uropod 3 composed of peduncle only *Metoediceros*
Uropod 3 with 1-2 rami 2
2. Uropod 3 with 1 ramus *Notoediceros*
Uropod 3 with 2 rami 3
3. Gnathopods well developed 4
Gnathopods mittenform or inferior 6
4. Epimera 1-3 with many marginal setae *Patuki*
All setae, if present, on epimera 1-3 facial, not marginal 5
5. Gill of coxa 5 small or vestigial, primary flagellum of antenna 1 with diverse armament, male and female gnathopods diverse *Exoediceros*
Gill 5 ordinary, armament of primary flagellum on antenna 1 homogeneous, gnathopods of both sexes alike *Exoediceroides*
6. Molar feeble *Exoediceropsis*
Molar strong 7
7. Inner plate of maxilla 1 naked, maxilla 2 lacking facial or submarginal inner row of setae, dactyls of pereopods 3-6 vestigial *Bathyporeiapus*

Inner plate of maxilla 2 widely setose, maxilla 2 with submarginal facial inner setal row, dactyls of pereopods 3-6 ordinary *Parhalimnedon*

KEY 2 TO THE GENERA

1. Male gnathopods with spine fields on hands near apices of dactyls 2
Male gnathopods lacking propodal spine fields 3
- 2a. Uropod 3 with 2 rami *Exoediceros*
b. Uropod 3 with 1 ramus *Notoediceros*
c. Uropod 3 lacking rami *Metoediceros*
3. Gnathopods ordinary, large 4
Gnathopods mittenform or gnathopod 2 almost simple couplet 6 of Key 1
4. Epimera 1-3 with many marginal setae *Patuki*
All setae of epimera 1-3, if present, facial
..... *Exoediceroides*

Genus *Notoediceros* Bousfield 1983

1983 *Notoediceros* Bousfield, p. 274.

TYPE SPECIES: *Notoediceros tasmaniensis* Bousfield 1983.

DIAGNOSIS: Body not carinate. Eyes paired, separate. Article 3 of peduncle on antenna 1 half as long as or shorter than half length of article 1. Fully articulate, scale-like accessory flagellum present. Primary flagellum of antenna 1 composed of similar articles bearing similar armaments. No articles of antenna 2 especially swollen. Calceoli absent. Mandibular incisor projecting, toothed; molar large, tritritative; palp 3-articulate, article 2 straight, article 3 clavate, stubby. Inner lobes of lower lip distinct, separate, fleshy. Outer plate of maxilla 2 with thin, slightly submarginal distinct spine, but lacking a single thick spine distinct from others. Plates of maxilla 2 slightly diverse. Anterior coxae strongly setose, coxae 1-4 rounded below, coxa 4 with posteroventral lobe. Gnathopods sexually diverse, in each sex similar to each other, subchelate; wrists not weakly lobate, not guarding hands; palms oblique, well defined, hands in female with sparse spines near apex of closed dactyl but in male with weakly developed spine fields. Dactyl of pereopods 3-4 obsolescent. Coxal gill 5 large. Article 2 of pereopod 7 expanded but scarcely lobate. Uropod 2 not reaching far along uropod 1; uropod 3 uniramous, peduncle not elongate, armed with large marginal spines; single ramus short. Telson entire, thick and fleshy but articulate.

RELATIONSHIP: *Notoediceros* appears to have ancestors similar to *Exoediceros* with which it shares numerous characters: most mouthparts, generalities of antennae, gnathopods, pereopodal dactyls, pleopods, uropods 1-2; and of course, familial characters. *Notoediceros* differs from *Exoediceros* in the loss of calceoli and aesthetascs on the antennae, the strongly bent bases of major spines and the reduction of 3 other spines on the outer plate of maxilla 1, the loss of lobe extensions on the wrists (carpi) of the gnathopods, the large gill of coxa 5, the bilobate condition of all the gills, and the loss of the inner ramus of uropod 3. These same distinc-

tions are generally applicable to *Exoediceroides* which is distinguished from *Exoediceros* in the keys above.

Metoediceros, which is closely related, differs from *Notoediceros* in the reduction of uropod 3 to a small vestige, the lack of an accessory flagellum, the lack of a mandibular palp and the poorly setose inner plate of maxilla 1.

Exoediceropsis differs from *Notoediceros* in the feeble molar, the feeble, mitten-shaped gnathopods, the marginal setae of epimera, the unsetose inner plate of maxilla 1, and the small outer plate of the maxilliped.

Bathyporeiapus differs from *Notoediceros* in all except the last of the features just cited. *Parhalimnedon* differs from *Notoediceros* in its feeble molar, its feeble mitten-shaped gnathopods, the long uropod 3 with long peduncle, the presence of 2 rami on uropod 3, and the absence of eyes.

The male of *Patuki* is unknown, but the third uropod of the female bears 2 rami and has an unarmed peduncle; and the eyes are closer together dorsally than those of *Notoediceros*.

Notoediceros tasmaniensis Bousfield 1983

Figs. 1-4

1983 *Notoediceros tasmaniensis* Bousfield, 275, fig. 2 (part).

DESCRIPTION OF MALE 'p': Each eye moderately pigmented. Ommatidia clear apically. Lateral cephalic lobes small, mammilliform, subacute.

Antennae short, extending subequally, articles of flagella short, bead-like, proliferate, lacking calceoli and aesthetascs; flagellum of antenna 1 with 12 articles, of antenna 2 with 10 articles, in both cases apicalmost article tiny.

Epistome flat in front; upper lip poorly separated from epistome, in lateral view protruding in front, rounded or subtruncate below, with dense anterior stiff brush. Incisors toothed; right lacinia mobilis 3-pronged, prongs serrate; left lacinia mobilis with 3 teeth; rakers stout, right and left about 8 each; molar stout, cuboid but strongly tritritative; palp stout, article 1 short, article 2 expanded and strongly setose, article 3 clavate, setae = ABCDE. Inner plate of maxilla 1 fully setose medially, outer plate with 11 spines (not all shown on all illustrations), several spines basally bent, 3 spines very small; palp strongly setose, 2-articulate. Plates of maxilla 2 slightly diverse, broad, inner with full oblique facial row of setae. Inner plates of maxilliped with medial margins appressed and bent orally, setose, apices each with 3 small medial spines and numerous widely spread setae; outer plates longer than inner, medially spinose; dactyl unguiform, with several setules on inner margin.

Coxae 1-4 progressively less setose; some setae on coxae 1-3 especially stout and often in ranks or submarginal; coxa 1 strongly rounded below, apically expanded, densely setose; coxa 2 narrower than 1, 3 as broad as 1, both more weakly setose; coxa 4 very broad and more elongate than anterior coxae, with weak but

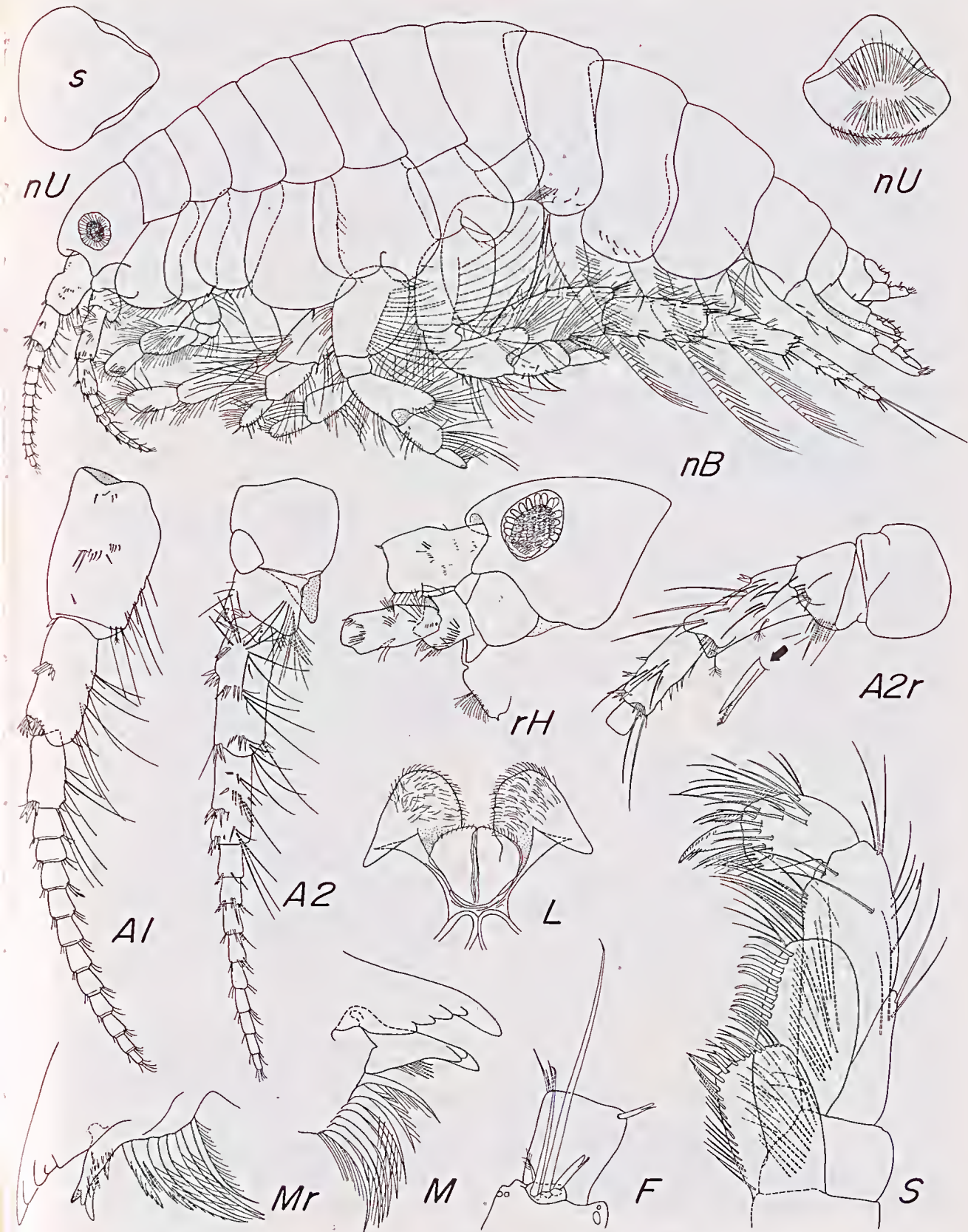


Fig. 1—*Notoediceros tasmaniensis*, unattributed figures, male 'p'; n, female 'n'; r, male 'r'.

pointed posteroventral lobe, poorly setose below; coxa 5 scarcely shorter than coxa 4, posterodorsal margin minutely castellate. Gnathopod 2 slightly larger than 1, both weakly twisted in preserved state, wrist of gnathopod 2 longer than that of gnathopod 1, both densely setose laterally, with strong axial row of setae medially, posterior lobes obsolescent, these margins armed with about 10 very stout, curved, pectinate spines; spine field of hand on gnathopod 2 about 14 count. (Article 2 of gnathopod 1 with 2 long posterior setae and 4 medial; of gnathopod 2 with 7 posterior, 1 posteroventral and 1 anteroproximal long setae.)

Dactyls of pereopods 3-4 vestigial, each bearing ordinary setule of normal dimensions, dwarfing dactyl; article 2 of pereopods 3-4 with strong anteromedial vertical row of long setae, both margins of article 6 spinose but anterior margin with multiple rows of spines. Pereopods 5-6 bearing small dactyls with largely absorbed apical nail and large setule; dactyl of pereopod 7 elongate, armed on both margins, apex with long and short spines; article 2 of pereopods 5-7 with midfacial lateral ridge, medial faces with many seriate ranks of filamentous setae in vertically oriented tiers. Gills present on coxae 2-6, flat, unpleated, bigeminous, with transverse capillaries.

Pleopods similar, peduncles elongate, each with 2 feeble retinacula, each outer ramus with posterior tooth or boss on article 1 apparently serving as clasp to lock with inner ramus; basal to each outer ramus, peduncle with small hook-like boss to hold ramus from apparent excessive backward motion; outer and inner rami about 1.5 and 1.3 times respectively as long as peduncles, outer and inner rami with about 20 and 16 articles respectively; each inner ramus with 4-5 basal clothespin setae (with apical pincer-fork).

Epimera 1-3 each with several anteroventral marginal setae; epimeron 1 with distinct facial ridge well above armaments, face below ridge with 9 stiff, wire-like setae and one similar seta apparently on medial surface; epimeron 2 lacking ridge, with 8 facial wire-like setae in rows of 8 and 5 horizontally, epimeron 3 bearing only weak posteroventral notch armed with setule, epimera 1-2 with similar setule well above ventral margin; posteroventral corners of epimera 1-3 rounded.

Urosomite 1 with 2 weak dorsal humps and small posteroventral protrusion; urosomites 2-3 each with unelevated posterodorsal edge; urosomite 3 barely elevated. Peduncle of uropod 1 with basofacial row of setae and spinule, dorsolateral margin naked except for apical spine, medial margin with 3 small spines, ventromedial face with several setae mostly in pairs; peduncle of uropod 2 with 1 apical dorsal spine, 1 similar apicomedial spine; rami of uropods 1-2 all with 4 apical spines, outer rami with 3 and 2 spines on dorsal margins, inner with double rows of 2-3 and 1-2 (lateral cited first) on uropods 1-2. Peduncle of uropod 3 short, with apical ring of 5 dorsal spines and basomedial dorsal group of 4 spinules and setule; ramus longer than peduncle, with complex of spines making ramus appear thorny, spines in 5 groups, 2 semicircles of 5 and 6 and apical group of

6 spines, medial margin with 2 groups of one spine each in tandem. Telson very short, broader than long, apex rounded, subtruncate, each dorsolateral face with 2 pairs of penicillate setules.

Cuticle very minutely punctate, occasionally with bare shallow pit bearing bulbar setule, punctations occasionally arranged into fingerprint striation pattern familiarly found in amphipods, this pattern especially prominent on backside of fleshy telson and lower posterior faces of epimera; bulbar setule pits especially prominent on dorsal surface of all segments, head, rostrum and article 1 of antenna 1.

FEMALE 'n': Generally like male but gnathopods distinct and brood plates present. Primary flagellum of antenna 1 with 9 articles; flagellum of antenna 2 with 7 articles. Gnathopod 1 like that of male but hand more slender and more rectangular, palm relatively shorter than in male and lacking spine fields near apex of dactyl; hand of gnathopod 2 similar to gnathopod 1 in stated attributes, wrist (carpus) relatively much longer than in male and longer than hand.

Brood plates and gills illustrated for this female; gills divided into 2 parts; brood plates (oostegites) generally slender, that of coxa 5 stoutest; note that setae of brood plates are rudimentary in this female but a fully setose brood plate for female 't' is illustrated as an example of the sexually active stage.

Appendages generally more sparsely armed than in male but this feature typical of smaller individuals of both sexes; for example, epimeron 1 with 8 facial setae, epimeron 2 with 6 (in different pattern); peduncle of uropod 1 with 2 basolateral spines, 2 ventral setal groups; non-terminal spine counts on rami of uropods 1, outer ramus 2, inner, 2 lateral, 2 medial; uropod 2, outer ramus 2, inner, 0 lateral, 1 medial. Uropod 3 (Fig. 4nR3), ramus with spine groups of 3-3-4.

MISCELLANEOUS SPECIMENS: Largest and best developed specimen is male 'q', in which flagella of antenna 1 are 12-articulate; of antenna 2, 9-articulate; and the accessory flagellum, in contrast to smaller individuals, is completely articulate. Setae on coxae 1-4 number 40-16-11-2, respectively; on epimera 1-2, 12 and 9. Basolateral armament on peduncle of uropod 1 consists of 1 seta-2 setae-1 spine. Dorsal uropodal spines on uropod 1 outer and inner rami are 4 and 2-2; on uropod 2, 2 and 1-2; on uropod 3 ramus 5-7-5 with detached medial pair in tandem of 1-1.

Male 'r', setae of epimera 1-2 are 7-8; male 's', 6-8 (in groups of 4-4); male 'o', 8-7.

Male 'o' is unusual in the presence of a middorsal spine on peduncle of uropod 2; spines on uropod 1 outer and inner rami are 3 and 2-2; on uropod 2, 2 and 2-2; ramus of uropod 3, 4-5 and 1-1 medial tandem (opposite uropod 3 variant, 5-5 and 1-1).

Young female 'u', brood plates rudimentary, setae on epimera 1-2, 7 and 6; spines on uropod 1 outer and inner rami, 2 and 2; on uropod 2, 2 and 1; ramus of left uropod 3, 1-4-3, right, 0-4-3.

Notes on carcass of holotype, male, 9.0 mm. (No

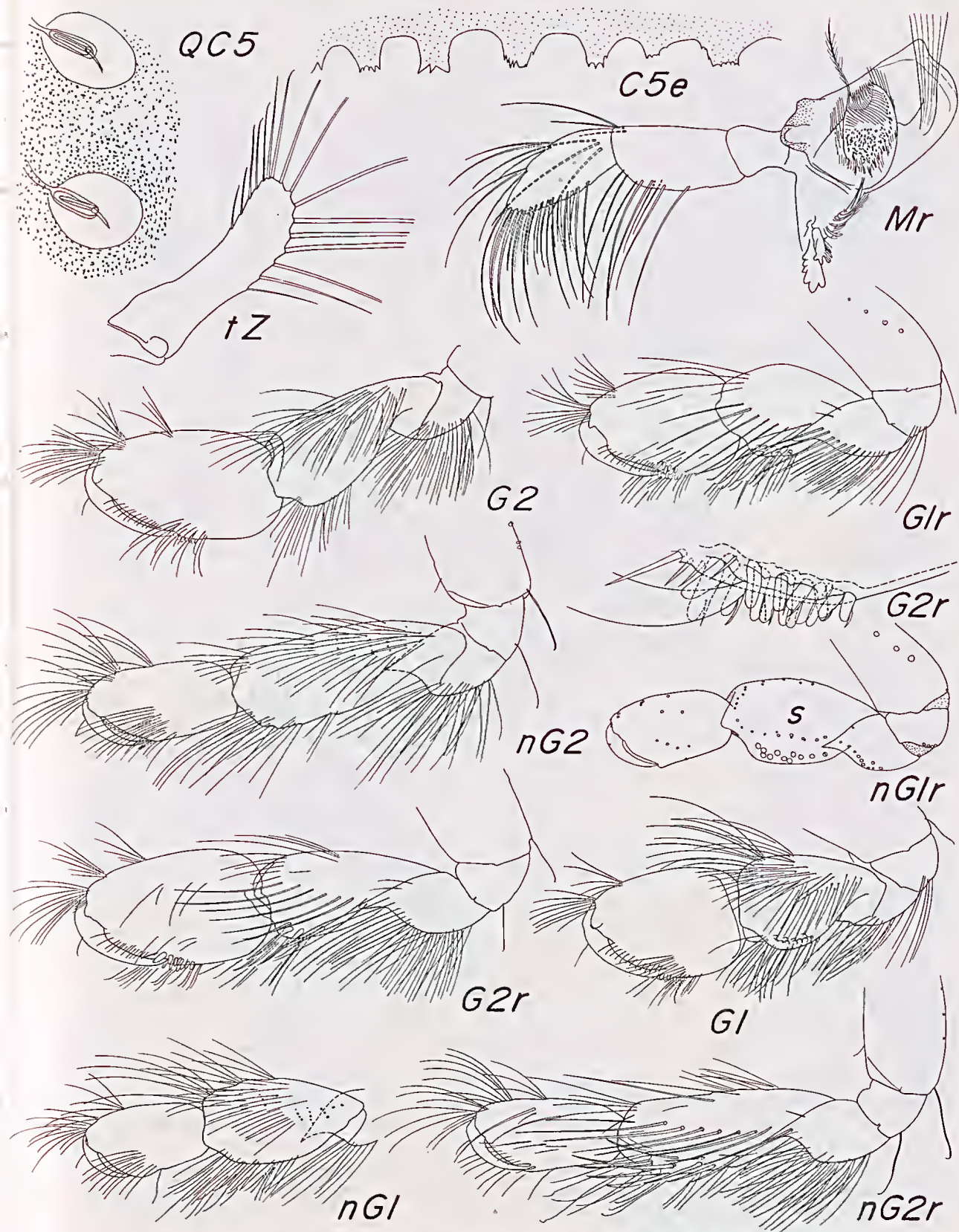


Fig. 2—*Notoedicerot tasmaniensis*, unattributed figures, male 'p'; n, female 'n'; t, female 't'.

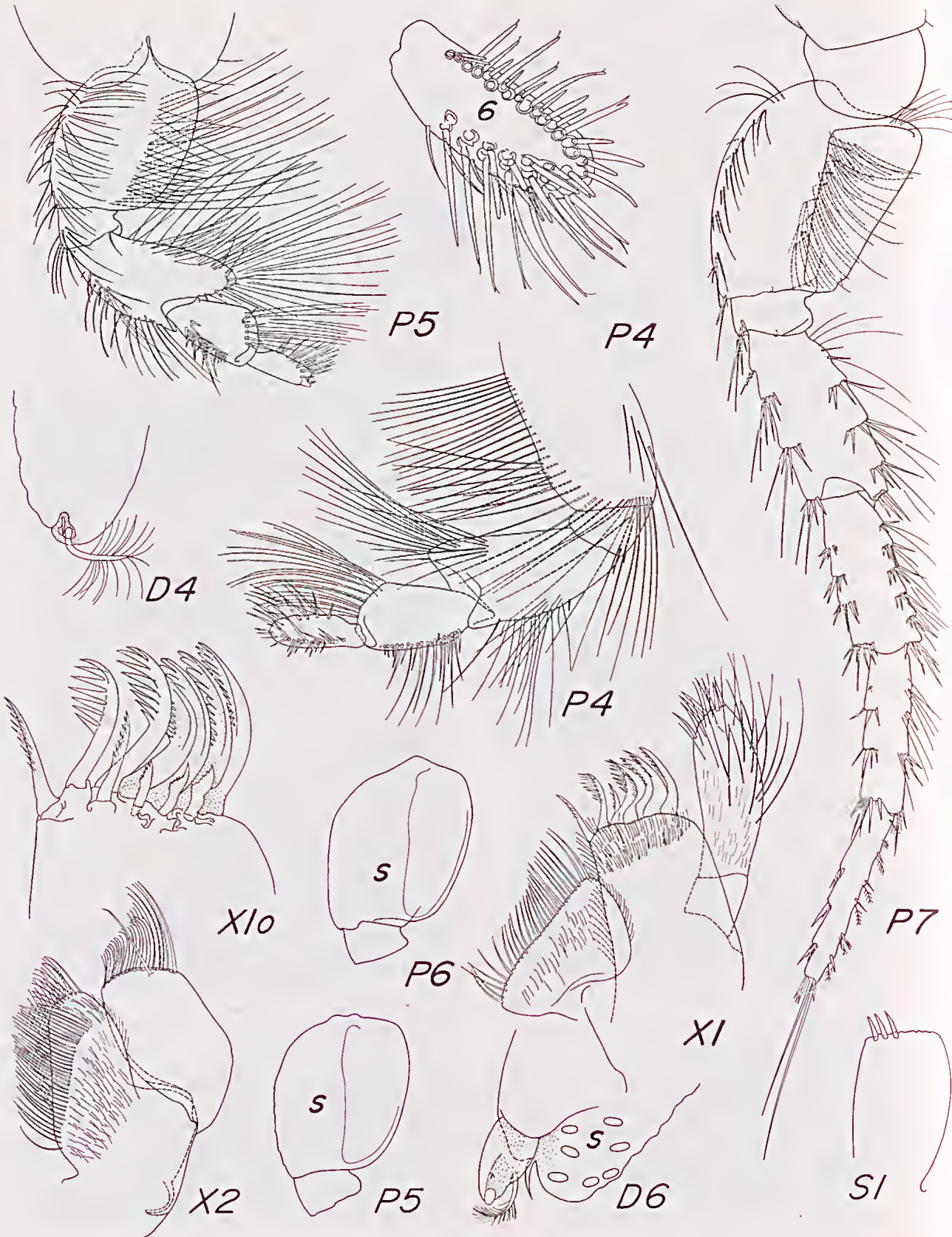


Fig. 3—*Notoedicerus tasmaniensis*, all figures, male 'p'.

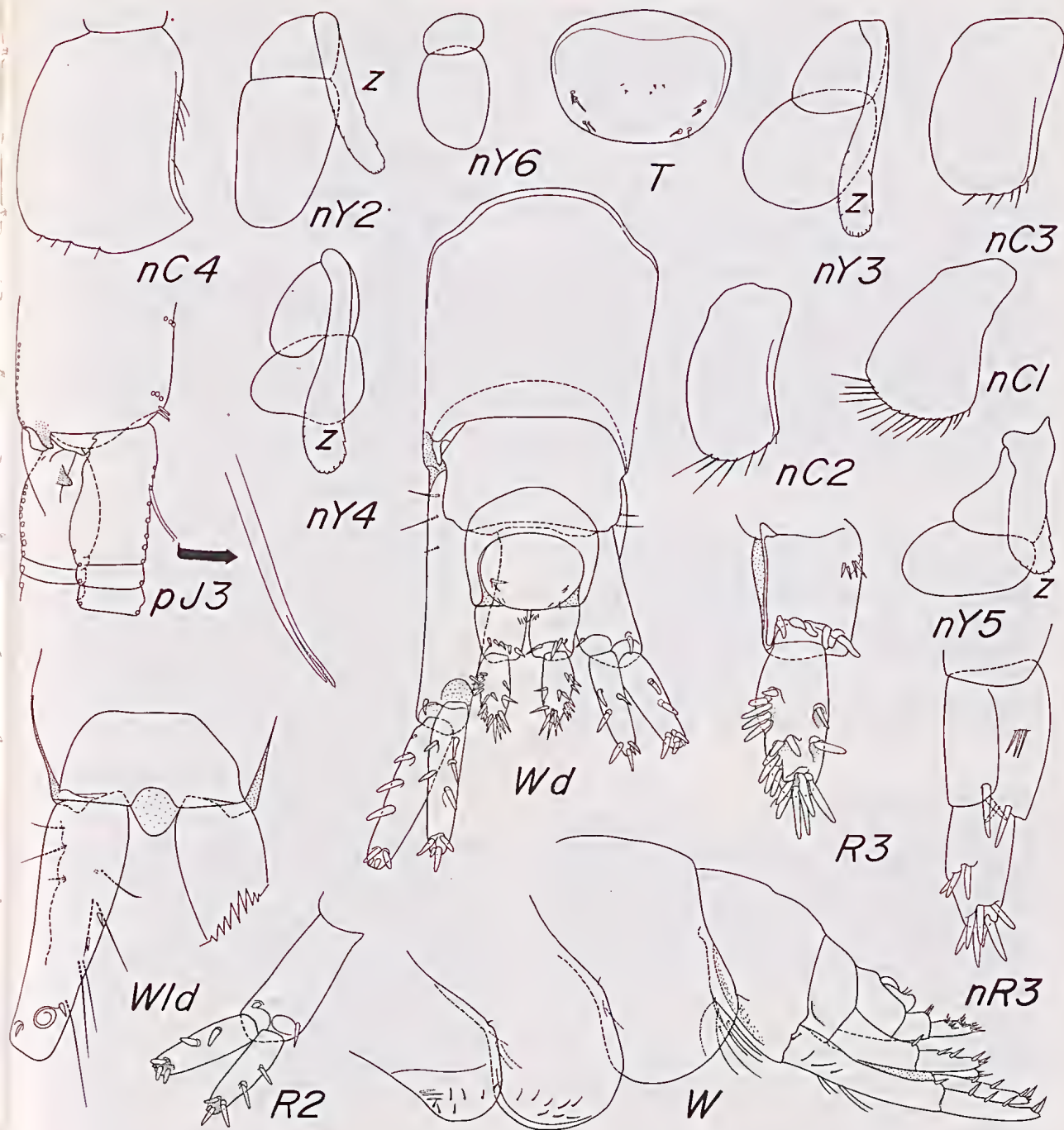


Fig. 4—*Notoediceros tasmaniensis*, unattributed figures, male 'p'; n, female 'n'.

slides.) Uropod 3 uniramous (like Fig. 4R3). Telson much more ovate transversely than shown by Bousfield (Fig. 4T).

VARIABILITY: Largely in setal densities, especially in presence of both lateral and medial dorsal spines on the inner rami of uropods 1-2 in larger specimens.

HOLOTYPE: Male, 9.0 mm, in collection of Museum of Victoria.

TYPE LOCALITY: Tasmania, west coast, Open Beach, in freshwater stream outflow, near high-water level, 7 Nov. 1978, Coll. E. L. Bousfield and A. M. M. Richardson.

VOUCHER MATERIAL: Tasmania, north end of Bond Bay, Point Davey, in brackish pools, 10 April 1975, collected by D. Coleman and J. Fenton: male 'p' 7.28 mm, female 'n' 5.50 mm (illustrated), male 'o' 6.01 mm, male 'q' 7.29 mm (noted as largest specimen), male 'r' 6.60 mm, male 's' 5.93 mm, female 't' 5.66 mm (oostegite illustrated), young female 'u' 4.22 mm.

REMARKS: In describing this genus, Bousfield (1983) noted an 'unequally biramous' uropod 3, but our examination of the holotype and paratypes demonstrates the uniramous condition (Figure 4R3). We have not dissected the carcass of the holotype (no slides have, as yet, been lodged) but find it conforms to our description in other characters. Bousfield's diagnosis of the genus stated 'weakly (or not) calceolate antennae (male only)'. The holotype of the type-species lacks calceoli, which Bousfield in a sentence below uses as one of three main characters distinguishing this genus from others in its subgroup. Our key develops other relationships.

DISTRIBUTION: Tasmania, marine brackish pools and streams of intertidal zone.

Exoediceroides Bousfield 1983

1983 (March) *Exoediceroides* Bousfield, p. 273.

1983 (June) *Warreyus* Barnard & Drummond, p. 65.

TYPE SPECIES (by original designation): *Exoediceroides maximus* Bousfield 1983. (= *Oediceros latrans* Haswell 1879).

OTHER SPECIES: *Exoediceros maculosus* Sheard 1936 (type species of *Warreyus* Barnard & Drummond 1983)

ACKNOWLEDGEMENTS

Our material came from a Survey conducted in 1975, with the assistance of an ABRS grant, by the Zoology Department of The University of Tasmania (Dr P. S. Lake); thanks are due to that institution for making available the material, and to D. Coleman and J. Fenton who collected it.

We also thank Caroline Cox Lyons of New York City for inking our drawings.

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PAST AND PRESENT DISTRIBUTIONS AND
TRANSLOCATIONS OF MURRAY COD *MACCULLOCHELLA*
PEELI AND TROUT COD *M. MACQUARIENSIS* (PISCES:
PERCICHTHYIDAE) IN VICTORIA

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ABSTRACT: Details of past and present distributions and translocations of Murray cod and trout cod in Victoria are presented. Because of the similarities between the two species and their overlapping distributions there is a great deal of uncertainty about many of the early records which simply refer to 'cod'. Nevertheless, it is evident that Murray cod have undergone only a marginal reduction in their natural geographical range, but have declined markedly in abundance, whereas trout cod have declined dramatically both in distribution and abundance. Translocations to outside the natural geographical range of Murray cod, particularly in the Wimmera and West Wimmera regions, have expanded the range of this species. However, as in the Murray-Darling system, the stocks in these areas have also declined. Trout cod are now considered endangered and Murray cod vulnerable. It is suggested that any attempts to rectify this situation must include a stocking programme using hatchery-bred fish, together with active habitat management in selected areas.

Victorian tributaries of the Murray River and that part of the Murray River contiguous with Victoria support natural populations of several species of native freshwater sport-fish, but the present distributions of these species differ markedly from their past, natural distributions. Man-made changes in the physico-chemical characteristics of the Murray-Darling system, together with the detrimental effects of overfishing and introduced fish, have caused an overall depletion of native fish stocks to such an extent that some species are now rare or seriously threatened with extinction (Lake 1967, 1971, 1978; Berra 1974; Reynolds 1976; Cadwallader 1977, 1978, 1981; Llewellyn & MacDonald 1980; Pollard *et al.* 1980; Clarke 1981).

As a prerequisite for effective restocking programmes and to assist in the conservation and management of the present stocks of native fish in Victoria, it is necessary to have information on the past and present distributions and translocations of each species. Such data have recently been collated for Macquarie perch (Cadwallader 1981) and in this paper we summarise similar data for two other members of the Percichthyidae, the Murray cod *Maccullochella peeli* (Mitchell 1838) and the trout cod *M. macquariensis* (Cuvier 1829). Both species are endemic to the Murray-Darling River system and have been keenly sought by both commercial and recreational fishermen (Dakin & Kesteven 1938; Berra & Weatherley 1972; Cadwallader 1977; Llewellyn & MacDonald 1980). However, the distribution and abundance of both species have declined since the advent of European man in Australia and Murray cod are now caught infrequently and trout cod very rarely.

METHODS

Information on the distributions of Murray cod and trout cod in Victoria was obtained from the following published works: Wilson (1857), Lake (1971, 1978),

Anon. (1973, 1974, 1980, 1981), Berra (1974), Harrington (1974), Cadwallader (1977, 1979, 1981), Tunbridge (1978, 1980), Walker & Hillman (1977), Llewellyn & MacDonald (1980), Pollard *et al.* (1980), Scott *et al.* (1980), Clarke (1981) and Tunbridge & Rogan (1981), and from the records of the Australian Museum, the National Museum of Victoria and the Fisheries and Wildlife Division of the Ministry for Conservation, from Fisheries and Wildlife officers throughout Victoria and from discussions with anglers.

RESULTS

The past and present distributions of Murray cod and trout cod in Victoria (including that part of the Murray River contiguous with Victoria) are shown in Figs 1 and 2, respectively. The present distribution of Murray cod (solid circles and squares in Fig. 1) is similar to its past distribution (solid and open circles in Fig. 1), except for the addition of populations derived from translocated fish in the Wimmera area and the disappearance of natural populations in waters such as Lake Cooper (locality 31) and the upper reaches of the Loddon, Campaspe and Goulburn River systems. In contrast, the present distribution of trout cod (solid circles and squares in Fig. 2) is much more restricted than in the past (solid and open circles in Fig. 2).

Details of known translocations of Murray cod and trout cod in Victoria are listed in Table 1.

Since 1978, Murray cod bred by the Fisheries and Wildlife Division at its Warmwater Fisheries Station Pilot Project at Lake Charlegrark (Cadwallader *et al.* 1979) have been stocked in farm dams throughout the State (crosses in Fig. 1) and in Lake Nillahcootie, Lake Meering, Loch Garry, Taylors Lake, Walpolla Creek and the Wimmera River (Table 1). For several years Murray cod produced at the New South Wales Inland Fisheries Research Station at Narrandera have been pur-



Fig. 1—Past and present distributions of Murray Cod in Victoria. The grey shaded area indicates the presumed past, natural distribution of Murray cod; ●, natural population still present (post 1970); ○, natural population, but no recent records; ■, population derived from introduced fish with post 1970 record(s) and/or post 1970 translocation(s); □, introduced, but no recent records; +, hatchery-bred fish introduced into farm dams, post 1978. Key to locality numbers: 1, Corryong Creek (lower reaches); 2, Cudgewa Creek (lower reaches); 3, Cudgewa Creek (middle to upper reaches); 4, Murray River (Towong Upper to Lake Hume); 5, Lake Hume; 6, Mitta Mitta River (Dartmouth Dam to Lake Hume); 7, Dartmouth Dam and inflowing waters; 8, Kiewa River (lower reaches) and tributaries; 9, Murray River (Hume Weir to Yarrawonga); 10, Ovens River (lower reaches)—Punt Creek; 11, Ovens River (Gapstead to Bundalong); 12, Lake Sambell; 13, Ovens River (Bright to Gapstead); 14, Buffalo River (lower reaches); 15, Buffalo River (upper reaches); 16, King River (lower reaches); 17, King River (Cheshunt to Edi); 18, Lake Mulwala; 19, Murray River (Yarrawonga to Yielima); 20, Broken Creek (lower reaches); 21, Goulburn River (Shepparton to Murray River) and associated irrigation channels; 22, Loch Garry; 23, Broken River (lower reaches); 24, Broken River (Benalla); 25, Lake Mokoan; 26, Lake Nillahcootie; 27, Seven Creeks (upper reaches); 28, Seven Creeks (lower reaches); 29, Goulburn River (Lake Nagambie to Shepparton); 30, Waranga Basin; 31, Lake Cooper; 32, Lake Nagambie-Goulburn Weir; 33, Hughes Creek (Ruffy to Bungle Boori); 34, Hughes Creek (lower reaches); 35, Goulburn River (Seymour to Lake Nagambie); 36, Sunday Creek (Broadford); 37, King Parrot Creek; 38, Yea River; 39, Goulburn River (Lake Eildon to Trawool); 40, Lake Eildon and inflowing waters; 41, Murray River (Yielima to Gunbower); 42, Campaspe River (Rochester to Murray River); 43, Campaspe River (Lake Eppalock to Rochester); 44, Campaspe River (upper reaches); 45, Coliban River; 46, Gunbower Creek; 47, Lake Boga; 48, Kerang Lakes (Kangaroo, Charm, Cullen, Raecourse and the three Reedy Lakes); 49, Little Murray River; 50, Loddon River (Kerang to Murray River); 51, Pyramid Creek; 52, Kow Swamp; 53, Loddon River (Durham Ox to Kerang); 54, Lake Meering; 55, Little Lake Meering; 56, Loddon River (Bridgewater to Durham Ox); 57, Serpentine Creek; 58, Waranga Western Channel; 59, Loddon River (Laanecoorie Reservoir to Bridgewater); 60, Cairn Curran Reservoir; 61, Expedition Pass Reservoir; 62, Loddon River (upper reaches); 63, Deep Creek (=Tullaroop Creek); 64, Avoca River (Charlton); 65, Avoca River (Charlton to Emu); 66, Avoca River (Emu-Bealiba area); 67, Murray River (Gunbower to Tooleybuc); 68, Murray River (Tooleybuc to South Australian border); 69, Walpolla Creek; 70, Lindsay Creek; 71, Lake Hindmarsh; 72, Wimmera River (Jeparit); 73, Wimmera River (Antwerp); 74, Wimmera River (Dimboola); 75, Wimmera River (Horsham); 76, Wimmera River (Glenorchy); 77, Green Lake; 78, Taylors Lake; 79, Marma Lake; 80, Ashens Creek; 81, Richardson River; 82, Wooroonooke Lakes; 83, Lake Jil Jil; 84, Lake Charlegrark; 85, Big Boorookpi Swamp; 86, Nowhere Else Swamp; 87, Lake Carpolac; 88, Lake Collins; 89, Miga Lake; 90, Skipton Reservoir; 91, Yarra River (Healesville to Dights Falls); 92, dams, Doncaster; 93, Blackburn Lake; 94, Fish hatchery at Studley Park; 95, Plenty River; 96, Yan Yean Reservoir; 97, Watts River-Maroonadah Reservoir; 98, Yarra River (Launching Place).



Fig. 2—Past and present distributions of trout cod in Victoria. The grey shaded area indicates the presumed past, natural distribution of trout cod; ●, natural population still present (post 1970); ○, natural population, but no recent records; ■, population derived from introduced fish, still present; □, introduced, but no recent records. Key to locality numbers: 1, Corryong Creek; 2, Cudgewa Creek (lower reaches); 3, Cudgewa Creek (middle to upper reaches); 4, Murray River (Tintaldra to Lake Hume); 5, Lake Hume; 6, Mitta Mitta River (Dartmouth Dam to Mitta Mitta); 7, Dartmouth Dam and inflowing waters; 8, Murray River (Lake Hume to Lake Mulwala); 9, Lake Mulwala; 10, Ovens River (Peechelbar); 11, Lake Sambell; 12, Ovens River (Tarrowingee); 13, Buffalo River (lower reaches); 14, Buffalo River (upper reaches); 15, King River (Cheshunt); 16, Murray River (Lake Mulwala to Strathmerton); 17, Murray River (Barmah Lakes); 18, Goulburn River (Shepparton to Murray River) and associated irrigation channels; 19, Broken River (lower reaches); 20, Seven Creeks (lower reaches); 21, Seven Creeks (upper reaches); 22, Hughes Creek (lower reaches); 23, Hughes Creek (upper reaches); 24, Goulburn River (Cathkin); 25, Goulburn River (Eildon to Thornton); 26, Lake Eildon; 27, Campaspe River (lower reaches); 28, Campaspe River (upper reaches); 29, Coliban River; 30, Murray River (Swan Hill); 31, Murray River (Nyah to South Australian border).

chased privately and released in farm dams in Victoria (crosses in Fig. 1); some have also been purchased by angling clubs and released in public waters such as Lake Meering (Table 1). All public waters stocked in recent years are either located within the natural geographical range of Murray cod or in areas where this species has previously been stocked.

DISCUSSION

Although commercial and recreational fishermen have distinguished between Murray cod and trout cod for quite some time, e.g. see Cadwallader (1977), it is only recently that the trout cod has been scientifically recognised as a distinct species from Murray cod (Berra

& Weatherley 1972; Berra 1974; MacDonald 1978). Because of the physical similarities between the two species and their overlapping distributions in the Murray-Darling system there is a great deal of uncertainty about many of the early distributional records which simply refer to 'cod'.

The 50 'Murray cod' transferred from the Ovens River to Lake Sambell in 1928 (Table 1) were probably all or mostly trout cod. The source locality, the upper reaches of the Ovens River near Brookfield, is within the natural range of trout cod and this species of cod has been the only one taken to date in Lake Sambell. Similarly, the 43 'Murray cod' and 57 'cod' taken in the Goulburn River at Cathkin in 1921 and 1922 respectively

TABLE 1
TRANSLOCATIONS OF MURRAY COD AND TROUT COD IN VICTORIA
Parentheses indicate localities outside the natural geographical range of each species; TL, total length

Release locality			Source locality			Remarks	
Name of water	Ref. No. (Fig. 1)	Catchment	Date	Name of water	Ref. No. (Fig. 1)		
(Ashens Creek	80	Wimmera River)	1972	(Lake Charlegrark	84	West Wimmera)	5-12 June; 50 Murray cod, mean TL 140 mm, range 105-180 mm, from Lake Charlegrark released in Ashens Creek near Lubeck.
Avoca River	64	Avoca River	1972	(Lake Charlegrark	84	West Wimmera)	5-12 June; 100 Murray cod, mean TL 140 mm, range 105-180 mm, from Lake Charlegrark released in Avoca River at Charlton.
Avoca River	65	Avoca River	1972	(Lake Charlegrark	84	West Wimmera)	5-12 June; 400 Murray cod, mean TL 140 mm, range 105-180 mm, from Lake Charlegrark released in Avoca River between Emu and Bealiba.
Broken River	24	Broken River	1915	O'Tooles Dam	—	?	Feb.; 350 cod and perch from O'Tooles Dam released in Broken River at Benalla.
(Lake Carpolac	87	West Wimmera)	1969	(Lake Charlegrark	84	West Wimmera)	1131 Murray cod, TL range 70-150 mm, from Lake Charlegrark released in Lakes Collins, Miga, Green and Carpolac.
(Lake Charlegrark	84	West Wimmera)	1955	Murray River	?	Murray River	51 Murray cod from Murray River released in Lake Charlegrark.
(Lake Collins	88	West Wimmera)	1969	(Lake Charlegrark	84	West Wimmera)	1131 Murray cod, TL range 70-150 mm, from Lake Charlegrark released in Lakes Collins, Miga, Green and Carpolac.
Deep Creek = Tullaroop Creek	63	Loddon River	1935	Murray River	?	Murray River	April, 300 cod from Murray River released in Deep Creek in the Maryborough area.
Lake Eildon	40	Goulburn River	1983	Snobs Creek Hatchery	—	Goulburn River	20-22 April; 34 Murray cod, mean TL 513 mm, range 315-790 mm, mean weight 2132 g, range 300-7330 g, from Snobs Creek Hatchery released into the Delatite arm of Lake Eildon.
Expedition Pass Reservoir	61	Loddon River	?	Not recorded	—	—	No details available.
Loch Garry	22	Goulburn River	1982	(Lake Charlegrark	84	West Wimmera)	1 Dec.; 5000 hatchery-bred Murray cod fry ² , mean TL 12.7 mm, range 12.0-13.5 mm, released in Loch Garry.

(Green Lake	77	Wimmera River)	1969	(Lake Charlegrark	84	West Wimmera)	1131 Murray cod, TL range 70-150 mm, from Lake Charlegrark released in Lakes Collins, Miga, Green and Carpolac.
Hughes Creek	33	Goulburn River	1921 late 1920s	Goulburn Weir Seven Creeks	32 27	Goulburn River Goulburn River	March; 20 Murray cod from Goulburn Weir released in Hughes Creek at Ruffy. 17 trout cod from Seven Creeks released in dam adjacent to Hughes Creek; dam burst, releasing fish in creek between Dropmore and Terip Terip. 5-12 June; 200 Murray cod, mean TL 140 mm, range 105-180 mm, from Lake Charlegrark released in Lake Jil Jil.
(Lake Jil Jil	83	Wimmera River)	1972	(Lake Charlegrark	84	West Wimmera)	8 Murray cod from Murray River released in Marma Lake.
(Marma Lake	79	Wimmera River)	1955	Murray River	?	Murray River	16 Dec.; 1000 hatchery-bred Murray cod fry ³ released in Lake Meering.
Lake Meering	54	Loddon River	1978	Murrumbidgee River	—	N.S.W.	17 Dec.; 5000 hatchery-bred Murray cod fry ³ , mean TL 12.3 mm, range 11.5-13.5 mm, released in Lake Meering.
(Miga Lake	89	West Wimmera)	1969	(Lake Charlegrark	84	West Wimmera)	1131 Murray cod, TL range 70-150 mm, from Lake Charlegrark released in Lakes Collins, Miga, Green and Carpolac.
Lake Nillaheootie	26	Broken River	1982	(Lake Charlegrark	84	West Wimmera)	14 Dec.; 5000 hatchery-bred Murray cod fry ² , mean TL 16.7 mm, range 15.3-17.8 mm, released in Lake Nillaheootie.
(Nowhere Else Swamp	86	West Wimmera)	1972	(Lake Charlegrark	84	West Wimmera)	June; unknown number of Murray cod from Lake Charlegrark released in Nowhere Else Swamp.
(Plenty River	95	Yarra River)	1857	King Parrot Creek	37	Goulburn River	Murray cod from King Parrot Creek released in Plenty River; 14 on 6 Feb., 27 later in Feb., 25 in March.
(Richardson River	81	Wimmera River)	1972	(Lake Charlegrark	84	West Wimmera)	5-12 June; 200 Murray cod, mean TL 140 mm, range 105-180 mm, from Lake Charlegrark released in Richardson River above Guthries Weir.
Lake Sambell	12	Ovens River	1928	Ovens River	11	Ovens River	50 Murray cod ¹ , up to 0.9 kg, from Ovens River released in Lake Sambell, Beechworth.
Seven Creeks	27	Goulburn River	1921	Goulburn River	39	Goulburn River	May; 43 Murray cod ¹ taken at Cathkin on Goulburn River released in upper reaches of Seven Creeks system.

TABLE 1 (continued)

Release locality			Source locality			Remarks	
Name of water	Ref. No. (Fig. 1)	Catchment	Date	Name of water	Ref. No. (Fig. 1)		Catchment
			1921	Seven Creeks	28	Goulburn River	About 50 small cod ¹ and Macquarie perch taken in Seven Creeks system below Goomram Falls released upstream near Strathbogrie.
			1922	Goulburn River	39	Goulburn River	57 cod ¹ taken at Cathkin on Goulburn River released near Strathbogrie in the upper reaches of Seven Creeks system.
(Skipton Reservoir	90	Hopkins River)	1920	Not recorded	—	—	Dec.; 3 Murray cod, mean length 230 mm, released in Skipton Reservoir.
Sunday Creek	36	Goulburn River	1917	Not recorded	—	—	Jan.; 18 Murray cod released in Sunday Creek, Broadford.
(Taylors Lake	78	Wimmera River)	1933	Wakool River	—	N.S.W.	April; 88 cod and perch from Wakool River released in Taylors Lake.
			1935	Murray River	67	Murray River	Jan.; 38 cod from Murray River in the Gunbower area released in Taylors Lake.
			1935	Murray River	67	Murray River	April; 500-600 cod from Murray River in the Gunbower area released in Taylors Lake.
			1935	Not recorded	—	—	April; 50 cod and perch, TL range 254-432 mm, released in Taylors Lake.
			1936	N.S.W.	—	?	Jan.; 30 cod, mean length 279 mm, released in Taylors Lake.
			1937	Not recorded	—	—	Jan.-Feb.; 48 cod, mean length 330 m, released in Taylors Lake.
			1981	(Lake Charlegrark	84	West Wimmera)	8-9 Jan.; 6000 hatchery-bred Murray cod fry ² , mean TL 23.2 mm, range 20.8-25.4 mm, mean weight 0.15 g, released in Taylors Lake
			1982	(Lake Charlegrark	84	West Wimmera)	25 Jan.; 4000 hatchery-bred Murray cod fry ² , mean TL 19.2 mm, range 17.5-20.8 mm mean weight 0.08 g, released in Taylors Lake.
Walpolla Creek	69	Mallee	1982	(Lake Charlegrark	84	West Wimmera)	18 Dec.; 5700 hatchery-bred Murray cod fry ² , mean TL 12.1 mm, range 11.0-14.0 mm, released in Walpolla Creek.

(Watts River)	97	Yarra River)	1890s	?	—	?	Murray cod released in Watts River during the 1890s; no other details available.
(Wimmera River)	72	Wimmera River)	1982	(Lake Charlegrark	84	West Wimmera)	27 Jan.; 1200 hatchery-bred Murray cod fry ² , mean TL 19.2 mm, range 17.5-20.8 mm, mean weight 0.08 g, released in Wimmera River at Jeparit.
			1982	(Lake Charlegrark	84	West Wimmera)	20 Dec.; 2000 hatchery-bred Murray cod fry ² , mean TL 13.5 mm, range 12.6-14.9 mm, released in Wimmera River at Jeparit.
(Wimmera River)	74	Wimmera River)	c1950	Murray River	?	Murray River	333 Murray cod from Murray River released in Wimmera River at Dimboola.
			1969	(Lake Charlegrark	84	West Wimmera)	300 yearling Murray cod from Lake Charlegrark released in Wimmera River at Horseshoe Bend.
			1982	(Lake Charlegrark	84	West Wimmera)	29 Nov.-20 Dec.; 2000 hatchery-bred Murray cod fry ² , mean TL 13.2 mm, range 12.1-14.9 mm, released in Wimmera River at Dimboola.
			1983	(Lake Charlegrark	84	West Wimmera)	8 Jan.; 158 hatchery-bred Murray cod yearlings ² , mean TL 120.4 mm, range 62-178 mm, mean weight 26.9 g, range 4.1-76.4 g, released in the Wimmera River at Dimboola.
Wimmera River	75	Wimmera River)	1938	Murray River	?	Murray River	April; 38 cod and Macquarie perch from Murray River released in Wimmera River.
			1948	Kyalite River	N.S.W.	Murray River	60 Macquarie perch and Murray cod, mean weight 2.3 kg, released in Wimmera River.
			1949	Murray River	?	Murray River	March; 300 Murray cod, length 102-178 mm, from Murray River released in Wimmera River.
			1982	(Lake Charlegrark	84	West Wimmera)	10 Nov.; 104 hatchery-bred Murray cod yearlings ² , mean TL 77.8 mm, range 40-136 mm, mean weight 9.7 g, range 1.0-39.9 g, released in the Wimmera River at Horsham.
			1982	(Lake Charlegrark	84	West Wimmera)	30 Nov.-20 Dec.; 2000 hatchery-bred Murray cod fry ² , mean TL 13.1 mm, range 12.1-14.9 mm, released in Wimmera River at Horsham.

TABLE 1 (*continued*)

Release locality			Source locality			Remarks	
Name of water	Ref. No. (Fig. 1)	Catchment	Date	Name of water	Ref. No. (Fig. 1)		
Wimmera River	76	Wimmera River	1972	(Lake Charlegrark	84	West Wimmera)	5-12 June; 100 Murray cod, mean TL 140 mm, range 105-180 mm, from Lake Charlegrark, released in Wimmera River above Glenorchy.
(Wooroonooke Lakes	82	Wimmera River)	1972	(Lake Charlegrark	84	West Wimmera)	5-12 June; 100 Murray cod, mean TL 140 mm, range 105-180 mm, from Lake Charlegrark, released in Wooroonooke Lakes.
(Yan Yean Reservoir	96	Yarra River)	?	?	—	?	No details available.
(Yarra River	91	Yarra River)	1909	Not recorded	—	—	Nov.; 1 cod, length 203 mm, weight 142 g, tagged (No. 72) and released in Yarra River at Studley Park.
			1920	Not recorded	—	—	Dec.; 15 Murray cod, mean length 152 mm, released in Yarra River at Studley Park.
			1960	Not recorded	—	—	Several juvenile cod caught in N.S.W. released in Yarra River. No other details available.
			?	?	—	?	Murray cod released in Yarra River at Launching Place. No details available.
Miscellaneous lakes and ponds in or near Melbourne. (Blackburn Lake	93	Yarra River)	1922	Goulburn Weir	32	Goulburn River	11 Feb.; 22 Murray cod, length 152-203 mm, released in Blackburn Lake.
(dams, Doncaster	92	Yarra River)	1920	Not recorded	—	—	Dec.; 16 Murray cod, mean length 230 mm, released in Petty's dams (2), Doncaster.
(Fish Hatchery, Studley Park	94	Yarra River)	1927	Goulburn Weir	32	Goulburn River	24 Nov.; 36 Murray cod from Goulburn Weir sent to Hatchery.

¹ Although some of the original fish may have been Murray cod, recent investigations by the Fisheries and Wildlife Division suggest that most were trout cod.

² Produced at the Warmwater Fisheries Station Pilot Project, Lake Charlegrark (Fisheries and Wildlife Division, Victoria).

³ Produced at the Inland Fisheries Research Station, Narrandera (New South Wales Department of Agriculture).

and translocated to above the Gooram Falls in the upper reaches of the Seven Creeks system (Table 1) were most likely trout cod. Trout cod presently occur in the upper reaches of the Seven Creeks system, whereas Murray cod do not (Cadwallader 1979). In addition to the fish from the Goulburn River, in 1921 a further 50 'cod' were taken from the Seven Creeks system below the Gooram Falls and released above the falls, in the Strathbogie area. Records indicate that 'cod' were being caught in the lower reaches of the Seven Creeks system before 1921 and that Murray cod were present until quite recently. Therefore, it is possible that at the time of the 1921 translocation there were natural populations of both species of cod in the lower reaches of the Seven Creeks system.

MURRAY COD

The natural geographical range of Murray cod has not been greatly reduced, but recent records of their occurrence within this range are often anecdotal. Furthermore, these records often mention only a few or single individuals, some of which are very large specimens, suggesting that they may well be members of relict populations.

During the last five years several Murray cod have been taken during Fisheries and Wildlife Division surveys in the Kiewa, lower Delatite, Buffalo, upper Ovens, lower Goulburn and lower Broken Rivers. They have also been taken occasionally by anglers in some of the Kerang lakes, the Goulburn and Big River arms of Lake Eildon, the lower Goulburn, Ovens, Loddon and Campaspe Rivers and in that part of the Murray River contiguous with Victoria (Fig. 1). A single Murray cod has recently been taken in the Mitta Mitta River arm of newly-formed Lake Dartmouth, but the present status of the Murray cod population recorded by Tunbridge (1978) in a now-inundated stretch of river near the dam wall is unknown, although Murray cod are still taken occasionally in the Mitta Mitta River below the dam. It is likely that the present population of Murray cod in the Avoca River consists mainly of translocated fish and their progeny, since the last verified record prior to the release of cod from Lake Charlegrark in 1972 (Table 1) was of a fish angled in 1967. Thus, at present, it appears that there are very few Murray cod in the Avoca, Campaspe, Broken and Kiewa Rivers and only small populations in the Loddon, Goulburn, Ovens and Mitta Mitta Rivers and in the Murray River contiguous with Victoria and associated Victorian anabranches, swamps and lakes such as those at Kerang and Barmah. Reasons for the decline of Murray cod in the Murray system have been discussed elsewhere (Lake 1971; Reynolds 1976; Cadwallader 1978; Pollard *et al.* 1980).

Translocations of Murray cod from the Murray River to the Wimmera River at Horsham in 1938, 1948 and 1949 (Table 1) resulted in Murray cod moving downstream and, in subsequent years, being taken in the river at Dimboola, Antwerp, Jeparit and Lake Hindmarsh (Fig. 1). Despite further translocations of Murray cod from the Murray River to the Wimmera River at

Dimboola in about 1950 and from Lake Charlegrark to the Wimmera River above Glenorchy in 1972 (Table 1), it appears that only a relict population remains in the river. Murray cod are now taken infrequently in the Horsham, Dimboola and Antwerp areas.

Initially, the decline of the Murray cod populations in the Wimmera River and Lake Hindmarsh was probably caused by unreliable water flows, low water levels and man-made obstructions on the river. Weirs were constructed at Jeparit, Antwerp, Dimboola and Horsham and water was impounded in several tributaries for domestic and irrigation purposes. In more recent years, the Murray cod populations have declined even further because of problems associated with the destruction of available habitat by so-called 'river improvement' schemes. Water quality has also declined considerably and eutrophication is now an increasing problem in the lower reaches of the river. These problems are compounded by relatively high water temperatures during summer when water flow is most restricted.

The translocation of 51 Murray cod from the Murray River to Lake Charlegrark in the West Wimmera region in 1955 (Table 1) has resulted in the only known, viable, self-propagating population of the species outside its natural geographical range in Victoria. When Lake Charlegrark overflows, Murray cod move through a small drainage creek to Big Boorook Swamp, where they are also abundant. During 1969 and 1972, several translocations of Murray cod from Lake Charlegrark to various waters in the Wimmera and West Wimmera regions (Table 1) resulted in a population becoming established in Green Lake near Horsham. Of the other waters stocked, Miga Lake, Lake Carpolac and Nowhere Else Swamp have since periodically dried up, and few or no Murray cod have been taken in Lakes Jil Jil, Woornoonoke and Collins or in Ashens Creek and the Richardson River.

Of the other waters outside the natural range which have been stocked with Murray cod (apart from recent releases of hatchery-bred fish), both Taylors Lake near Horsham and the Yarra River between Dights Falls and Warrandyte still support small populations (Table 1). Very low water levels in the late 1960s, together with heavy angling pressure at the time, are thought to have caused the demise of the population in Taylors Lake.

According to local anglers, some Murray cod were included in a shipment of Murray fish released in Marma Lake, Murtoa, in 1955 (Table 1). It is also thought that fish from either Taylors Lake or Ashens Creek moved downstream through the Wimmera-Mallee irrigation system into the lake. A large Murray cod was found dead here in 1981.

The present status of populations of hatchery-bred Murray cod stocked in public waters and farm dams throughout Victoria since 1978 depends very much on the type of water stocked. Fish are known to have perished in many dams, some of which periodically dry up. In other dams, it is suspected that the cod have been eaten by predatory birds. However, some dams continue to support small populations of Murray cod. Several

Murray cod were taken in Lake Meering in 1981 and it is thought that these were hatchery-bred fish released in 1978 by a local angling club. It is not known whether sufficient numbers of fish have survived to form a viable population. The success of releases of hatchery-bred Murray cod fry by the Fisheries and Wildlife Division during 1981 and 1982 has yet to be assessed.

TROUT COD

In recent years, angling reports and Fisheries and Wildlife Division surveys have indicated the presence of trout cod in Lake Mulwala, Lake Hume, Lake Sambell, the Murray River between Strathmerton and Yarrowonga and upstream of Lake Hume, the Ovens, Buffalo, King and Mitta Mitta Rivers, Cudgewa and Corryong Creeks and the Seven Creeks system. Of these localities, it appears that only the Seven Creeks system and the Murray River between Strathmerton and Yarrowonga support viable populations of trout cod. However, further investigations may yet reveal the presence of small, self-propagating populations in the upper reaches of the Ovens and King Rivers and Cudgewa Creek.

According to Berra (1974), trout cod could only be collected consistently in two localities in Victoria: the Seven Creeks system and Lake Sambell. However, the Lake Sambell population was decimated following an unexplained fish kill in 1970 and few trout cod have been taken in the lake since then. Trout cod were recorded by Tunbridge (1978) in the Mitta Mitta River, in an area now inundated by Lake Dartmouth; the present status of this population is unknown. Records indicate that trout cod have disappeared completely from the lower reaches of the Murray River contiguous with Victoria (up to and including the Barmah Lakes), the Murray River between Lake Mulwala and Lake Hume, the Campaspe River system (including the Coliban River) and almost completely from the Goulburn River system (including Lake Eildon, the Broken River and the lower reaches of the Seven Creeks system). It is likely that trout cod also once occurred in the Kiewa River and in most of the major tributaries of the Ovens and Mitta Mitta Rivers; but there are no records to confirm this.

Apart from the effects of overfishing and man-made changes to the environment, trout cod have probably been adversely affected by introduced trout, although there is little substantial evidence to support this view. In the Seven Creeks system, trout cod and trout were found to occupy the same type of habitat (Cadwallader 1979). Furthermore, in aquaria, young trout cod establish well-defined territories similar to those established by trout, so that young trout cod and trout may compete for space on the stream bed. Also, since they take the same types of food and live in similar situations, they may also compete directly for food items. Butcher (1967) also indicated that trout probably eat small trout cod. From what is known about the habitat requirements of trout cod it may be said that in general a 'good trout stream' is also a good trout cod stream. Perhaps it is more than coincidence that the areas

formerly occupied by trout cod in north eastern Victoria, from where the species appears to have been almost eliminated, are areas which have been heavily stocked with trout.

CONCLUSIONS

Murray cod have undergone a marginal reduction in their natural geographical range, but have declined markedly in abundance, whereas trout cod have declined dramatically both in distribution and abundance. Consequently, in Victorian waters and the Murray River contiguous with Victoria, using the I.U.C.N. Red Data Book definitions (Holloway 1979) as modified by Ahern (1982), the trout cod must now be considered endangered (i.e. in danger of extinction) and the Murray cod vulnerable (i.e. likely to move into the endangered category in the near future if the factors causing its demise continue operating). Any attempts to rectify this situation must involve the implementation of a stocking programme using hatchery-bred fish of both species, together with active habitat management in selected areas.

ACKNOWLEDGEMENTS

We thank all those people who contributed information on the distribution of Murray cod and trout cod in Victoria. In particular, we thank Charles Barnham, Alan Baxter, Jim Crosier, Peter Dickinson, Nick Major, Ian May, Pat Sheridan, Owen Thomas (all members or former members of the Fisheries and Wildlife Division), John Paxton (Australian Museum), Martin Gomon (National Museum of Victoria) and members of 'Native Fish Australia'. We also thank John Cameron (Fisheries and Wildlife Division) for assistance in sorting through distribution records, staff of the New South Wales Department of Agriculture, Division of Fisheries, for information on Victorian releases of hatchery bred Murray cod from the Inland Fisheries Research Station, Narrandera, and Jim Pribble (Fisheries and Wildlife Division) for comments on the manuscript.

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GROUNDWATER SYSTEMS AND DRYLAND SALINITY IN A CATCHMENT NEAR BOHO, N.E. VICTORIA

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ABSTRACT: An investigation of groundwater systems related to secondary dryland salinity was carried out between March and September 1982 in a catchment on the northern slopes of the Strathbogie Ranges. A shallow aquifer, ranging in depth from 12 to 20 m, discharges water at fresh and saline seeps. The aquifer is characterised by relatively high hydraulic conductivities and consists of waters which display chemical equilibria with albite. Underlying the aquifer is a deeper groundwater system which shows chemical equilibria with kaolinite and comprises materials of low hydraulic conductivity. The groundwater discharge areas have not increased in size for over 50 years. Assuming steady-state conditions, a water balance was carried out which suggests that the seeps result from an increased groundwater recharge of 20 mm caused by the reduction in transpiration following clearing of a native, deep-rooted forest.

Secondary soil salinity in dryland agricultural areas is now recognised as a major problem in Australia. Peck *et al.* (1983) report that an estimated 4 260 km² are severely affected. Detailed reviews discussing the cause of dryland salinity may be found in Peck (1978), Malcolm (1982) and Conacher (1982), and summarised on an Australia-wide basis by Peck *et al.* (1983). It is estimated that in Victoria at least 90 000 ha of non-irrigated agricultural land are severely affected by secondary salinisation (Jenkin 1981). Victorian salinity research has been summarised in general terms by Mitchell *et al.* (1978) and in more detail by Jenkin (1979).

The problem in Victoria was first recognised by Downes (1949) in a study of erosion in the northeast of the state. Subsequently, Cope (1958) suggested that salts of cyclic origin, as analysed by Hutton and Leslie (1958), were transported to the valley floor by shallow subsurface drainage or throughflow. Rowan (1971) presented the first systematic and detailed study of dryland salting in Victoria, from the northwestern region of the state. He recognised two groundwater systems responsible for salinisation, namely a locally perched body within aeolian sediments, and a deeper regional aquifer. Rowan considered that clearing of the native mallee vegetation was responsible for mobilizing salts stored within the profile. These salts were subsequently redistributed by groundwater and accumulated at the soil surface.

The relationship between salinity and hydrogeologic properties of the Riverine plains has been discussed by Macumber (1969, 1978). Macumber revealed that the capacity of the deep leads had been exceeded due to the increased recharge within catchment areas. This resulted in saline seeps being formed following the rise in groundwater levels to within the capillary fringe across substantial areas of the Riverine plains.

In 1973 the Northern Slopes Land Deterioration Project was initiated by the Victorian Soil Conservation Authority to investigate the processes of erosion and dryland salinity (Jenkin & Irwin 1975). Detailed research was to be conducted only in Ordovician sedimentary terrain. Essential principles established from the detailed

investigation were used to interpret information gathered in other Victorian localities in which dryland salting was apparent. The report presented preliminary conclusions suggesting that clearing of native forests and their replacement with shallow-rooted annual pastures caused a marked decrease in evapotranspiration and a consequential increase in groundwater recharge.

Dyson and Jenkin (1981), Jenkin (1981) and Jenkin and Dyson (in press) subsequently presented the results of more detailed hydrologic studies. From an experimental catchment near Kamarooka, north of Bendigo, they suggested that saline groundwater, discharging at the break of slope between the Ordovician upland front and the Riverine alluvial plains, originates from increased annual recharge derived from the cleared slopes. Jenkin (1981) and Jenkin and Dyson (in press) have further shown that saline groundwater discharge is primarily the result of an upward movement of groundwater below saline seeps. This mechanism of groundwater discharge appears common in studies of dryland salting in Australia (Nulsen & Henschke 1981).

In the Shire of Violet Town, at the junction between the Riverine plains and the bedrock uplands, dryland salting was recognised as a significant agricultural problem by the local community (George 1982a). Consequently a catchment was chosen at Boho, 8 km southeast of Violet Town, in which hydrologic studies were carried out to determine the processes involved in dryland salinisation under geologic and geomorphic conditions different from those studied by Dyson and Jenkin at Kamarooka.

GEOLOGY AND LAND-USE

The study area is located on the northern slopes of the Strathbogie Ranges (Fig. 1). These slopes represent the junction between the Riverine alluvial plains and the uplands described by Jenkin (1981). The steep nature of the junction zone is geologically controlled by the late Devonian, igneous, quartz-biotite-hypersthene dacite (White 1953). The surface catchment has an area of 50 ha, a relative relief of approximately 200 m, and is

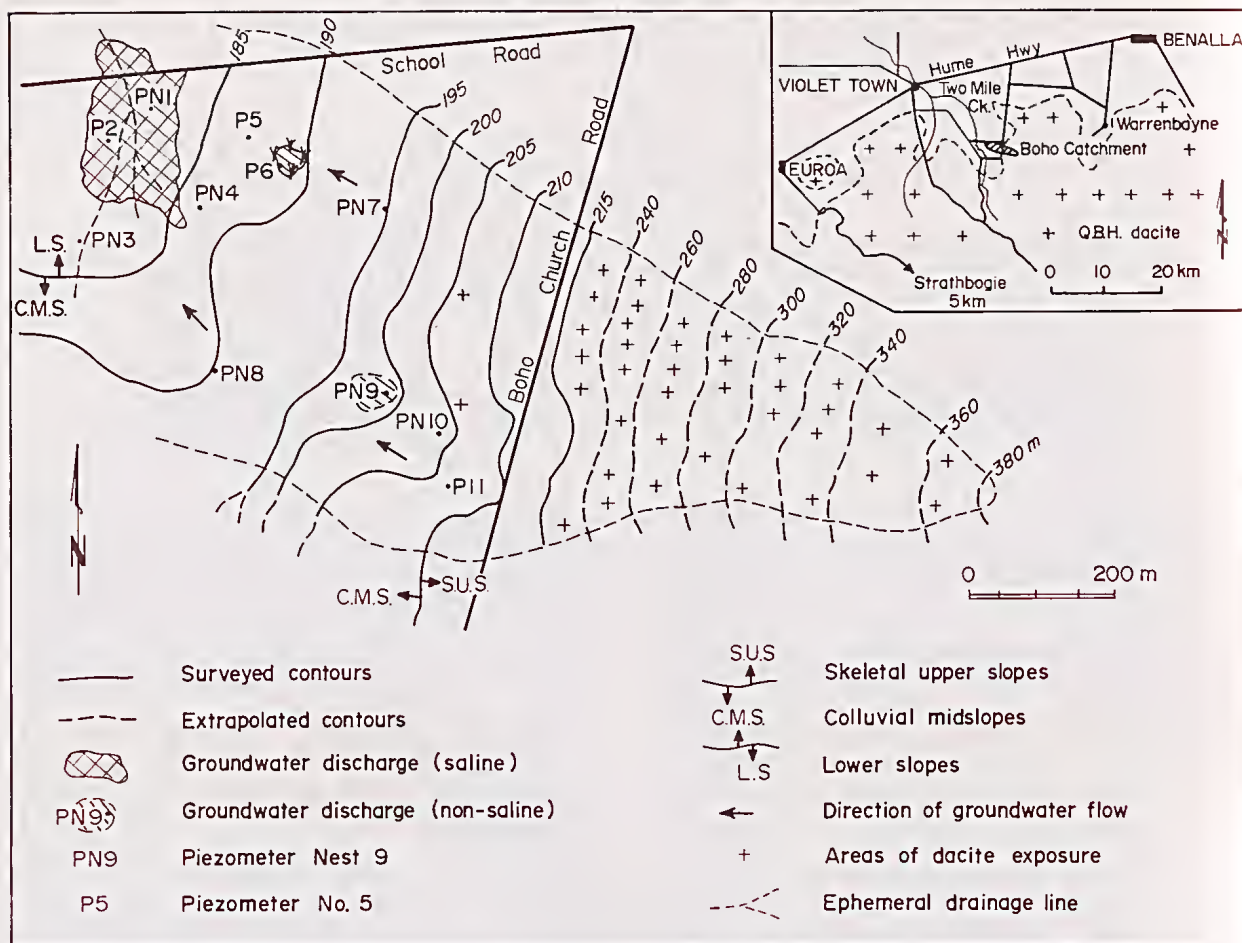


Fig. 1—Boho experimental catchment, N.E. Victoria.

the western face of a large spur which protrudes from the Ranges (Fig. 2). The salt-affected land and its local catchment, are located within the Two Mile Creek drainage basin. Its incised, ephemeral stream is located nearly a kilometre from the salt-affected area.

Clearing of the catchment occurred between 1875 and 1890, and only scattered remnants of the red box (*E. polyanthemos*) forest remain. Limited regrowth of sub-canopy species has occurred on the upper slopes, which are too steep for most agricultural activities. Pastures have remained unimproved and are dominated by onion grass (*Romulae rosea*) and capeweed (*Arthotheca calendula*) at the expense of native species. The area of dryland salinity has remained stable for at least 50 years, being first noticed in approximately 1920.

METHODS

A network of 27 piezometers was located in the catchment to monitor the groundwater systems. To assess the hydraulic properties of the saturated materials piezometers were installed in nests of three. The piezometer nests consist of a shallow (<5 m below

ground surface) intermediate (<10 m) and deep (<20 m) PVC tube slotted over the lower two metres for each depth interval.

Piezometer nests were located at lower, middle and upper slope sites, in such a pattern that groundwater isopotential maps could be prepared. All nests were west of the Boho Church Road as near-surface rock prohibited drilling east of the road.

Topographic and isopotential maps were prepared from surveyed spot-heights located throughout the lower- and mid-slopes of the catchment. On the upper slopes, east of the Boho Church Road (Fig. 1), surface catchment information was extrapolated from the Euroa 1:100 000 mapsheet (8035: edition 1), aerial photographic interpretation and field observations.

A standard 10 cm bucket auger was used to install the shallow piezometers in the saturated zone. Soil samples were collected at 0.5 m intervals to an average depth of four metres. Each sample was described using the techniques presented by Northcote (1971). Where possible samples were collected below this depth from the 'flights' of the Gemco power auger which was used to install the intermediate and deep piezometers. Im-



Fig. 2—The photo shows both the saline (centre-top) and non-saline (centre) groundwater discharge areas.

mediately drilling ceased, an appropriate length of slotted and capped 40 mm PVC pipe was inserted, the annulus around the pipe backfilled with washed sand screenings, and finally sealed above the slotted length with bentonite pellets. The remainder of the annulus was then filled with excavated materials and again sealed with a bentonite cap at the soil surface.

Values of saturated hydraulic conductivity were obtained from each piezometer using the Hvorslev, single well 'rate of rise' bailing technique (Hvorslev 1951). This method is recommended for application in materials with relatively low permeability (Hendry 1981).

Soil and water samples were analysed for electrical conductance (EC-mS m^{-1}), using the techniques discussed by Loveday (1974). The sampling of 1:5 aqueous extracts was conducted in April, 1982, while four water samples were analysed from each piezometer between April and August. A further 16 samples were analysed for Na, K, Mg, Ca, Fe, Cl, HCO₃, CO₃, NO₃ and SO₄. Hardness, as percent CaCO₃, as well as pH and electrical conductance were determined. An attempt was made to understand the thermodynamic and chemical equilibria conditions within the groundwater systems from the results of the chemical analyses. The method involves deriving ion activities according to the Debye-Huckel equation, and plotting appropriate values on equilibria-stability diagrams produced by Nesbitt (1977).

Values of mean annual precipitation and annual potential evaporation were extrapolated for the Boho catchment from field stations operated by the Bureau of Meteorology at Violet Town, Warrenbayne and Strathbogie. These stations are located within 20 km of the Boho catchment (Fig. 1).

RESULTS

CLIMATE

Precipitation at the catchment was estimated to have a mean annual value of 650 mm, while the potential annual evaporation rate was 1530 mm. A distinct seasonality exists with high evaporation rates and low rainfall in summer, while in the four winter months rainfall exceeds the potential evaporative demand. Although 860 mm of rain was recorded during 1981, the study period of 1982 received less than 30% of the mean annual rainfall. Field observations indicated that rainfall events of sufficient intensity and duration to produce surface runoff did not occur.

GEOMORPHIC UNITS

Three geomorphic units were identified within the catchment. The units are described as the upper, mid and lower slopes, with each type being separated by distinct gradient changes (Fig. 1). The lower and mid slope units comprise a complex association of alluvial

and colluvial sediments. The upslope soils appear to be developing *in situ*, although field observations identified some colluvial activity on the steeper slopes.

The upslope skeletal soils are coarse textured and uniform, grading from stony loams to loamy sands. These slopes are steep, ranging in slope angle from 6° to 24°. Rock outcrops and small cliffs are common features of this slope unit. Midslope colluvial soils are predominantly brown, gradational sandy clays while limited areas of yellow duplex profiles were also recognised near piezometer nest 6 (PN6). The midslope unit ranged in slope angle between 2° and 6°. The lower slope unit (<1°) occurs below the break of slope in the valley floor which corresponds with the salt-affected area. In this zone soils are brown, uniform, silty or sandy clays. The salt-affected area is extensively gullied and displayed salt efflorescence during most of the study period.

GROUNDWATER SYSTEMS

The hydraulic properties of the materials which comprise the groundwater systems are relatively anisotropic. The two zones can be distinguished by their differences in hydraulic properties, mineralogy, soil texture and physical conditions implied while drilling. The shallower materials, located to depths of 12 m in the lower slopes and to greater than 20 m at PN9, consist of sandy and silty clays. These sediments were saturated to near the surface in the salt-affected area (PN1) and at the upslope groundwater discharge area (PN9). It is considered that

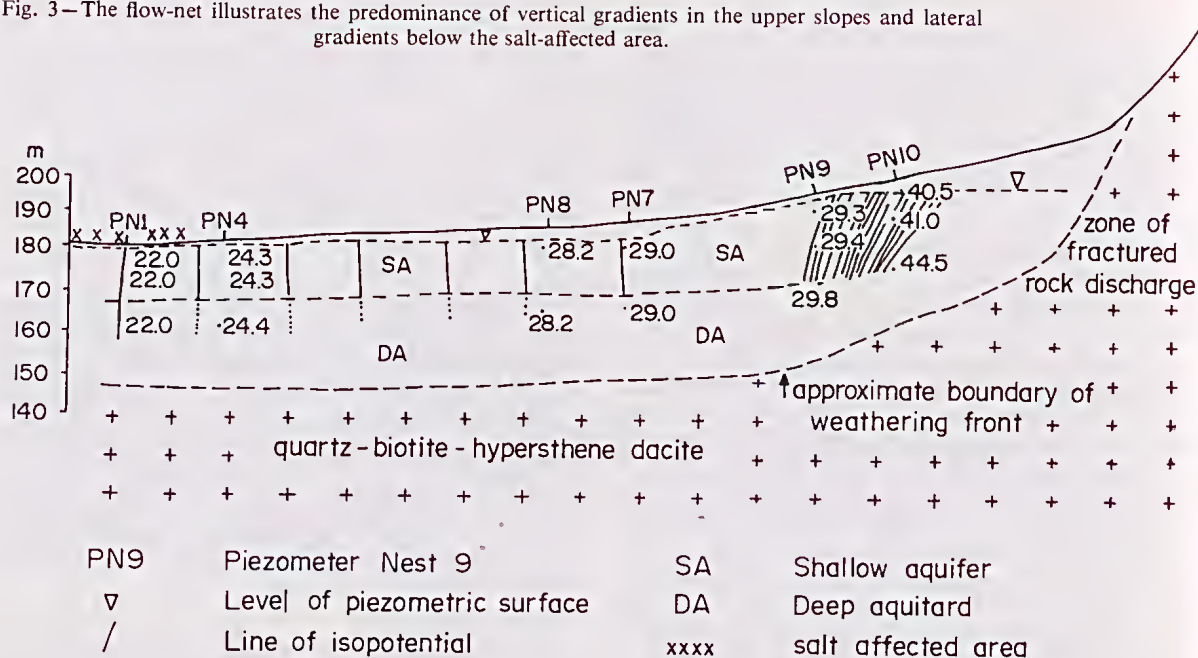
most of the groundwater within the shallow aquifer originates as discharge from the fractured dacite.

The deeper materials, consisting of heavy textured clays, form the deep groundwater system. This material is located at depths greater than 20 m at PN10 and greater than 12 m at PN1 and PN3. The total depth of the deep groundwater system is unknown; however, evidence from local bores suggests that weathering depths may range from 20 m to as much as 40 m in similar geomorphic environments.

HYDRAULIC CONDUCTIVITY

The hydraulic conductivities calculated from each piezometer reflect the textural dichotomy of the substrates as previously identified during drilling and sampling. The variation between the calculated values of saturated hydraulic conductivity from the deep and shallow groundwater systems exceeds two orders of magnitude. Hydraulic conductivities obtained from shallow and intermediate piezometers within the colluvial midslopes have representative values of 4.0×10^{-2} m/day. Limited evidence suggests that values derived from the intermediate piezometers have slightly higher hydraulic conductivities (6.0×10^{-2} m/day). However, the relative variation is insignificant when compared with the deep groundwater system. Mean hydraulic conductivities calculated from the deeper system provide a representative value of 5.0×10^{-4} m/day. The cumulative evidence suggests that an aquitard exists below a more permeable aquifer.

Fig. 3—The flow-net illustrates the predominance of vertical gradients in the upper slopes and lateral gradients below the salt-affected area.



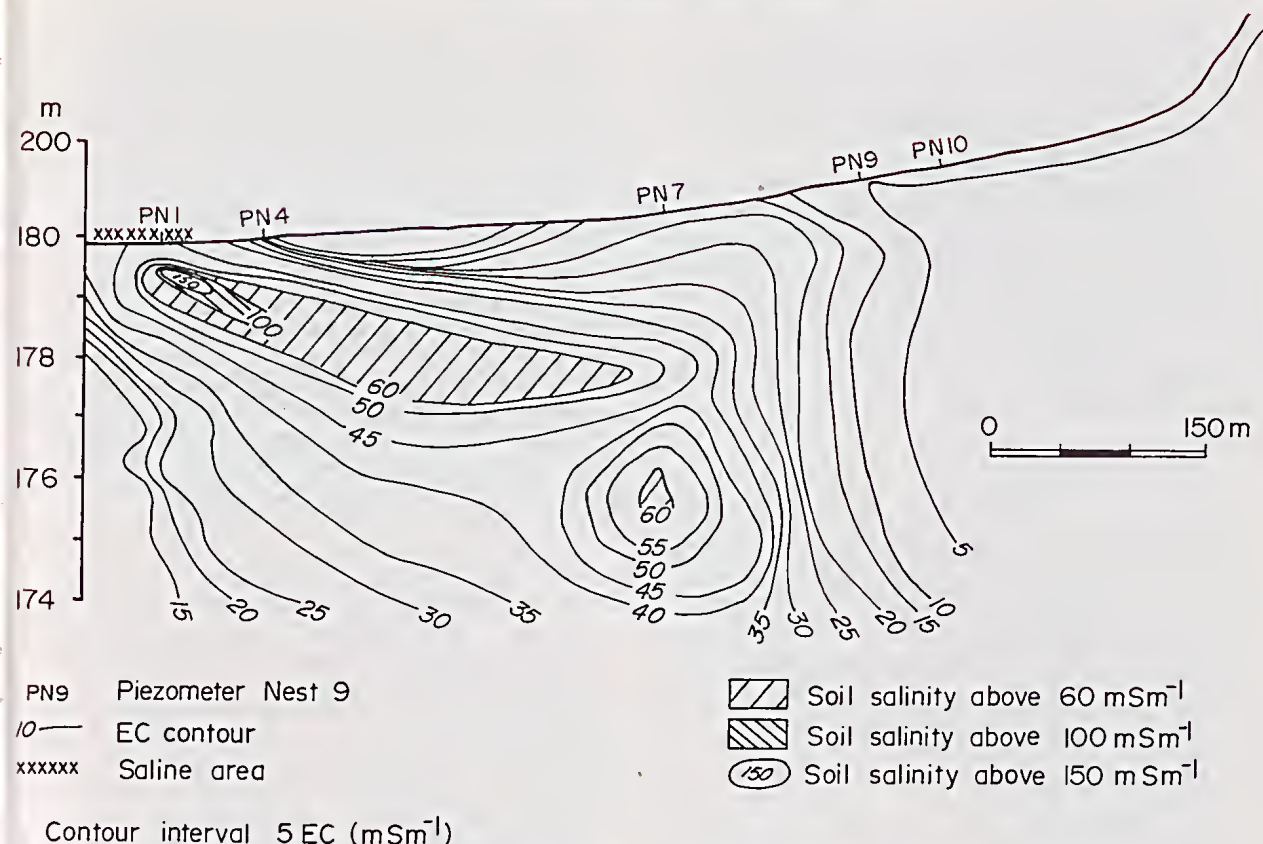


Fig. 4—Soil salinity contour profile showing the increase in soil salinity towards the groundwater discharge area.

Hydraulic conductivities ($3.0 \times 10^{-2} - 3.0 \times 10^{-3} \text{ m/day}$) obtained from the deep piezometers at the break of slope between the upper and midslopes (PN9 and PN10) reflect both the coarser material encountered, and the dominance of the shallow aquifer characteristics deeper in the profile and at higher levels in the catchment.

HYDRAULIC GRADIENTS

Lateral hydraulic gradients from the deep and shallow groundwater systems are dissimilar. Lateral gradients within the shallow aquifer approximate those of the surface topography, being 0.05 upslope and decreasing to 0.01 at the salt-affected area. In the deep groundwater system, lateral gradients near the break of slope between the upper and midslopes are very steep (0.07), reducing to 0.02 in midslopes and 0.01 in the lower slopes.

In order to present graphically the hydraulic properties of the catchment, a flow-net was constructed from the potentiometric data (Fig. 3). The flow-net indicates that groundwater discharge from the fractured dacite is under steep hydraulic gradients near PN9 and PN10. However, a uniform gradient exists in the mid and lower slopes. The flow-net further indicates that lateral flow is dominant in both the deep and shallow groundwater

systems, and that no upward pressure potential exists below the salt-affected area.

SOIL SALINITY

Soil salinities increase towards the salt-affected area (Fig. 4), and are concentrated towards the surface. The electrical conductivity (1:5 aqueous extracts) of samples ranges between 1.0 mS m^{-1} in the skeletal soils of the upper slopes and 150 mS m^{-1} near the surface at the salt-affected area. Conductivities of samples taken in the deep groundwater system range between 8.0 and 16.5 mS m^{-1} across the entire catchment, with the higher conductivities observed in the lower slopes. In contrast, values between 30 and 50 mS m^{-1} are common in the shallow groundwater system near the salt-affected area.

Three salt profile forms were delineated within the shallow soils ($< 5 \text{ m}$) of the catchment. The first displays a major zone of concentration, or bulge, below the soil surface. The second displays a steady increase with depth and the third a steady decrease with depth.

GROUNDWATER SALINITY

Within the shallow aquifer a marked increase in electrical conductivity was observed towards the salt-affected area, peaking at 1460 mS m^{-1} at PN4 (Fig. 5). Conductivities within the salt-affected area are

significantly lower (200-300 mSm⁻¹). A similar trend was observed within the deep groundwater system. In this zone two peak values occur at PN4 (450 mSm⁻¹) and PN7 (560 mSm⁻¹), but are significantly lower in all other locations, including the salt-affected area where salinity remains less than 100 mSm⁻¹.

Chemical speciation of the waters revealed that Na, HCO₃ and Cl are dominant in both the shallow and deep groundwater systems. Mg and Ca are minor species in all samples, with the exception of PN7, while SO₄, NO₃, CO₃ and K display consistently low concentrations. The importance of bicarbonate is reflected in the alkalinity of the groundwaters, which range from pH 7 to 10. Groundwater discharge at the soil surface has changed typical soil pH values from pH 5.1-6.4 to pH 8-9.

GROUNDWATER BALANCE

In order to quantify the hydrologic processes within the catchment an instantaneous groundwater balance was calculated. Several important assumptions were made on the basis of the experimental and field observations. The calculations assume that all the water is distributed by the shallow aquifer, and that the deeper system is not a source of groundwater discharge to the salt-affected area. Discharge by evaporation from a shallow water-table within the capillary fringe (and groundwater underflow) was considered to be in equilibrium with groundwater recharge, since the area of salt-affected land has remained stable over 50 years. This assumption considers that the area of groundwater discharge within the catchment is directly proportional to the area of groundwater recharge within the catchment.

Given these assumptions, a direct relationship may be drawn between recharge and discharge such that:

$$A_D (\text{ha}) \times D (\text{mm}) = A_R (\text{ha}) \times R (\text{mm}) \quad (1)$$

where D =discharge, A =recharge area or discharge area and R =recharge.

Groundwater flow towards the salt-affected area was calculated from Darcy's Law, using the Dupuit-Forchheimer assumptions at PN3 and P5. The results show that 3.21 Ml move towards the salt-affected area annually. The value of groundwater discharge at the surface was obtained by subtracting the annual quantity of flow which moves laterally beyond the discharge area. This flow component was estimated from known values of hydraulic conductivity and cross-sectional area, and was small (0.36 Ml yr⁻¹). In this case the hydraulic gradient was considered to reflect the surface topography between the salt-affected area and the Two Mile Creek, as no piezometers had been installed down-aquifer from the salt-affected area. Groundwater discharge at the salt-affected area was therefore calculated to be 2.85 Ml yr⁻¹.

The discharge of groundwater at the salt-affected area can easily be accounted for, since it represents only 4.4% of the total potential annual evaporation rate. Discharge was also apparent from two other locations within the catchment. Surface water within the 'spring-

fed' excavations was considered to evaporate at the potential rate, while discharge at PN9 was estimated at the fraction of the potential rate used above. Using the steady-state equation presented above (equation 1), it can be shown that approximately 20 mm of annual groundwater recharge is needed to maintain the discharge at the salt-affected area.

DISCUSSION

In reviewing the cause of saltland in Western Australia, Nulsen and Henschke (1981) and Malcolm (1982) reported that groundwater discharge is the result of evaporation from a shallow water-table. However, in these reviews it is noted that discharge results from upward hydraulic gradients from partially or semi-confined aquifers. In these cases it is argued that a potentiometric gradient forces water towards the surface. This feature is also noted in many physiographic regions of Victoria (Jenkin 1981).

At Boho no evidence was obtained to suggest that groundwater discharge at the salt-affected area is maintained by vertical hydraulic gradients. It is therefore considered that the presence of a saline area within the catchment is simply the result of a shallow water-table from which evaporation-induced, capillary rise occurs. However, the upslope groundwater discharge area (PN9) appears to be the result of steep vertical, hydraulic gradients of the sort mentioned by the authors noted above. At this location no salt-affected area exists as the groundwater salinity appears too low.

The assumption that 'catchment equilibrium' exists between recharge and discharge is based on the salt-affected area having remained stable for at least 50 years. On this basis it was assumed that a new hydrologic equilibrium had been developed between 30 and 50 years after clearing. This condition of equilibrium was seen to reflect a reduction in evapotranspiration resulting from the clearing of the deep-rooted native forest, and its replacement by shallow-rooted pasture species. It is therefore reasonable to infer that net groundwater recharge has increased as a result. The development of a salt-affected area in this case follows once water-tables rise to a level at which discharge takes place at the same rate as recharge.

The calculation of the rates of groundwater discharge (and hence recharge) are empirical first approximations. At Boho the existence of lateral flow within an unconfined aquifer suggests some difficulty in stating categorically that all water is discharged from the salt-affected area. It is conceivable that vertical hydraulic gradients may develop during seasonal periods of high potential evaporation near the surface of the shallow aquifer in the salt-affected area. However, neither the stratification of nested piezometers nor the research timetable allowed these factors to be considered. It is therefore concluded that in the light of the information available, based on interpolated hydraulic parameters, groundwater underflow leaving the catchment was a minor feature in the groundwater balance.

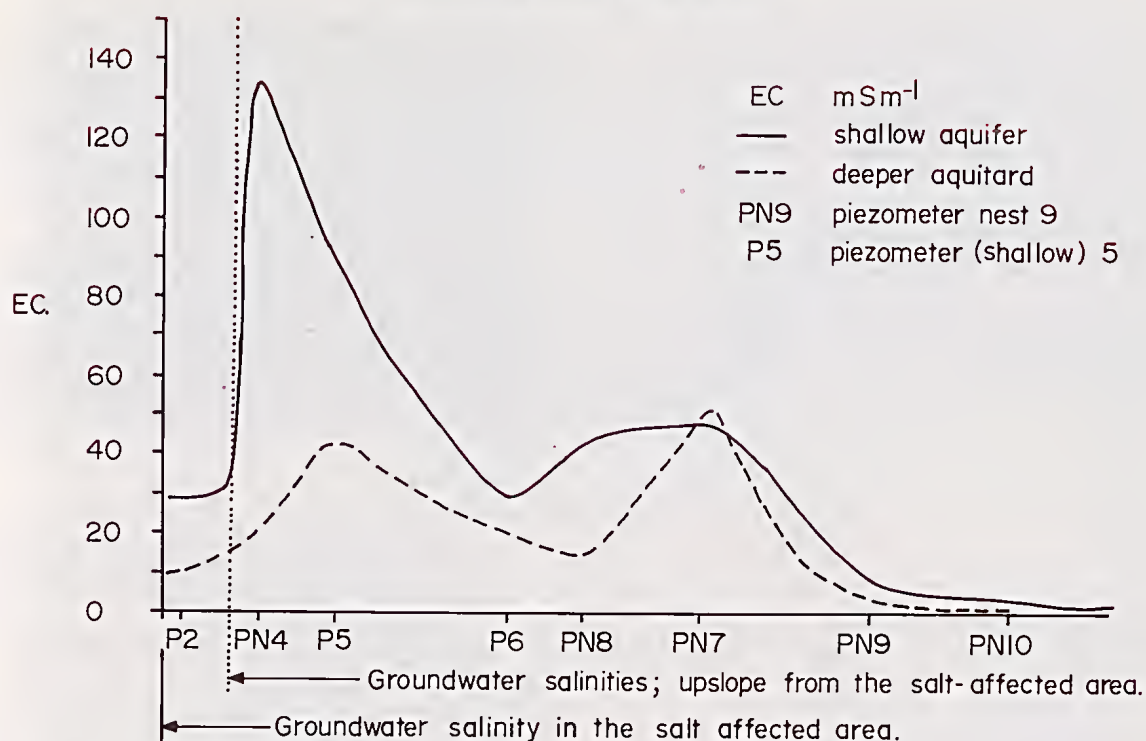


Fig. 5 — Groundwater salinity in each system increases towards the salt-affected area. The deeper system is considerably less saline than the shallower system.

The calculations would also appear to be validated since the potential evaporation rates create the ability for groundwater discharge to occur throughout most of the year. The results from the catchment groundwater balance would also appear to be similar to those obtained by Jenkin and Dyson (in press) at Kamarooka, north of Bendigo in central Victoria. At this location Jenkin and Dyson (in press) report that groundwater discharge is the result of 17 mm (5.7% of the annual potential evaporation rate) annual recharge. At Boho recharge rates were calculated to be approximately 20 mm, of 4.4% of the annual potential evaporation rate.

In order to provide further support for the contention that a distinctive two aquifer system exists the chemical composition of each groundwater system was compared. The technique applied required that ion-activity coefficients be computed from each chemical analysis, using the Debye-Huckel equation. It is recognised that this method can only be considered as a first approximation when delineating aquifer geochemistry; however, the results obtained were informative and deserve some comment. The equilibria conditions were inferred by analysing the results graphically, using Nesbitt's (1977) stability fields (Fig. 6). From these plots it may be inferred that the shallow system possesses groundwater that exhibits chemical equilibria between sodium-beidellite and albite whereas the deeper system indicates equilibria between kaolinite and sodium-

beidellite (P. Dyson pers. comm.). Further analysis of the thermodynamic nature of the aquifers was not considered, as the results correlated with the measured hydraulic parameters and clearly indicated the anisotropic nature of the groundwater systems.

Although the complexities of groundwater movement within the catchment require further analysis, several other similarities and differences were observed between the conditions under which dryland salting occurs at Kamarooka, discussed by Dyson and Jenkin (1981), Jenkin (1981) and Jenkin and Dyson (in press), and at Boho.

Within the Boho and Kamarooka catchments saline groundwater discharge was observed at the break of slope between valley alluvium and bedrock hills. However, at Boho, non-saline groundwater discharge was also apparent at the break of slope between the colluvial and upper-slope units. Discharge at this point is the result of steep vertical gradients, reflecting flow from the fractured-rock zone. However, unlike Boho, saline groundwater discharge in the lower slopes at Kamarooka is the result of strong vertical gradients below the seep. At Kamarooka the different geology, flatter topography and groundwater flow characteristics are believed to be significant in explaining the dissimilarities observed.

The similarity noted above between the recharge rate and the actual annual evaporation rate suggests that the differences which exist between the geologic and

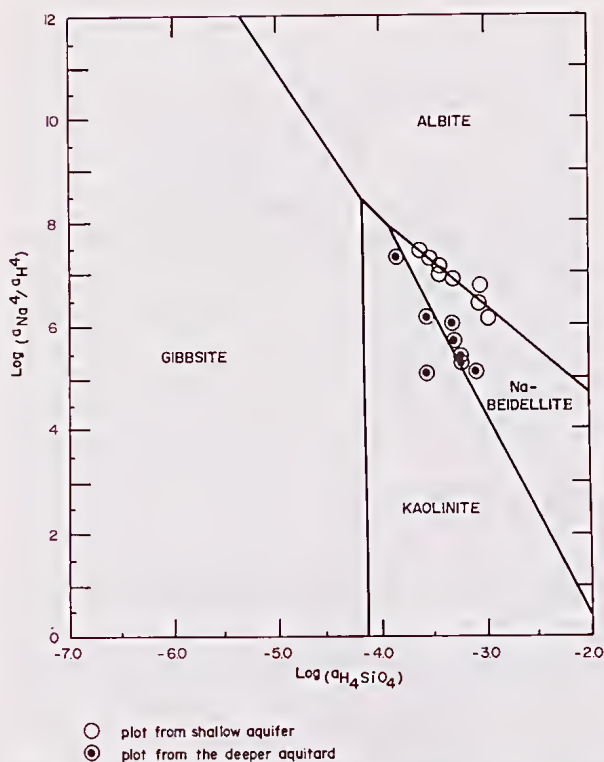


Fig. 6—The figure illustrates the different chemical characteristics of each groundwater system.

geomorphic environments are less significant than the hydrologic effects of reduced evapotranspiration following the clearing of native vegetation.

CONCLUSIONS

Two distinct groundwater systems were found within the Boho catchment. The volume of groundwater transported by the shallow aquifer was found to be 200 times greater than that of the deep groundwater system. Soil and water salinities vary between the fresher deep system, and the more saline shallow waters, increasing in both cases towards the salt-affected area. The anisotropic nature of the groundwater systems was further verified from the contrasting values of hydraulic conductivity and the differing chemical conditions within each system. Dryland salting within the catchment is produced by the evaporation of saline water ($200\text{--}300\text{ mSm}^{-1}$) from a shallow water-table ($<1.6\text{ m}$). Where fresh water ($<30\text{ mSm}^{-1}$) is discharged, no soil salinisation occurs, although similar surface characteristics were observed. Groundwater discharge at the soil surface by evaporation appears to be balanced by approximately 20 mm annual recharge to the aquifer.

The implication of low recharge values is important for catchment management procedures. Future forest or agricultural controls need therefore only increase water use in the recharge areas by a similar amount to restore productivity at the salt-affected area. At Boho it would

appear that beneficial results could be obtained by applying management controls to the skeletal soils in the upslope area. Future research should look to defining more precisely areas of preferential recharge so that management techniques might only disrupt a small proportion of the total area currently used for agriculture.

ACKNOWLEDGEMENTS

The author acknowledges the support provided by the Victorian Soil Conservation Authority, and in particular Mr Phil Dyson (Bendigo) for significant advice and help in analysing the geochemical nature of the groundwater systems. Dr Brian Finlayson (University of Melbourne) supervised the project whilst the Shire of Violet Town provided the impetus for the study's initiation.

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PROCEEDINGS
OF THE
ROYAL SOCIETY OF VICTORIA

Volume 96

NUMBER 2

ROYAL SOCIETY'S HALL
9 VICTORIA STREET, MELBOURNE 3000

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A NEW GENUS AND TWO NEW SPECIES OF
HAPLOSCLERID SPONGES (PORIFERA: DEMOSPONGIAE)
FROM THE TIMOR SEA, NORTHWEST AUSTRALIA

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ABSTRACT: Two new species of the Demospongiae order Haplosclerida are described, *Biminia macrotoxa* sp. nov. (Oceanapiidae), and *Acanthostrongylophora ashmorica*, gen. et sp. nov. (Petrosiidae), obtained from trawls off the northwest coast of Western Australia. Details are provided of other species obtained from the same collection, and held at the Museum of Victoria.

This paper presents descriptions of two previously undescribed sponges, one of which represents a new genus of the order Haplosclerida, both from the northwest coast of Australia. These species are part of a small collection of sponges made by Dr. C. C. Lu, aboard the R.V. *Hai Kung*, during March and April 1981.

The collection came from four localities in the Timor Sea: 1, North of Cape Londonderry, Joseph Bonaparte Gulf at 12° 39'S, 127° 04'E; 2, North of Penguin shoal, Holothuria Banks at 12° 51'S, 125° 44'E; 3, East of Montagu Sound, Bonaparte Archipelago at 13° 59'-14° 10'S, 124° 26'-55'E; 4, North of Barracouta shoals, Ashmore Reef at 12° 18'S, 124° 05'E. Specimens are housed at the Museum of Victoria, Melbourne (NMV) and fragments of each are stored at the Northern Territory Museum (NTM), Darwin. A fragment of one specimen is held at the Zoölogische Museum, Amsterdam (ZMA). Apart from the two new species described here, the collection contains the following sponges, (with locality: and NTM registration number). *Clathria coppingeri* Ridley (loc. 4: NTMZ1493), (Poecilosclerida: Microcionidae); *Echinodictyum asperum* Ridley and Dendy (3: NTMZ1486), and *E. mesenterinum* (Lamarck) (3: NTMZ1489), (Axinellida: Raspailiidae); an unrecognizable (partly macerated) *Oceanapia* sp. (3: NTMZ1482), (Haplosclerida: Oceanapiidae); *Callyspongia* (*Callyspongia*) sp. (4: NTMZ1494), (Haplosclerida, Callyspongiidae); *Psammocinia* sp. (3: NTMZ1485), (Dictyoceratida: Thorectidae); *Hippospongia* sp. (3: NTMZ1492), and *Hyatella* sp. (1: NTMZ1479), (Dictyoceratida: Thorectidae); *Dysidea* sp. (3: NTMZ1480), (Dictyoceratida: Dysideidae); *Lanthella flabelliformis* (Pallas) (2: NTMZ1497), (Verongida: Lanthellidae); *Caulospongia perfoliata* (Lamarck) (3: NTMZ1490), (Hadromerida, Suberitidae); 5 spp of *Cinachyra* (3: NTMZ1481, 1487, 1488, 1491; 4: NTMZ1496), and *Craniella* sp. (3: NTMZ1483), (Spirophorida: Tetillidae); *Corticum* sp. (3: NTMZ1484), (Homosclerophorida: Plakinidae). Previous records of sponges from the northwest coast and the North West Shelf of Western Australia are described elsewhere (Hooper in press). Terminology follows Van Soest (1980).

SYSTEMATICS

Order HAPLOSCLERIDA Topsent 1928
Family OCEANAPIIDAE Van Soest 1980
Genus *Biminia* Wiedenmayer 1977

Biminia macrotoxa sp. nov.
Figs 1-3

MATERIAL EXAMINED: Holotype NMVF51373 (NTMZ1478 fragment of holotype) from 120 naut. mls North of Cape Londonderry, Joseph Bonaparte Gulf, Timor Sea, Western Australia, lat. 12° 39'S, long. 127° 03'-06'E; Coll. C. C. Lu, R.V. *Hai Kung*, station no. 70032502, trawl, 88 m depth, 25 Mar. 1981. Paratype NTMZ1919 from Catalina Island, East Arm, Darwin Harbour, N.T., lat. 12° 29.5'S, long. 130° 54.5'E; coll. J.N.A. Hooper, SCUBA, 19 m depth, 9 Feb. 1984; mud-sand habitat.

DIAGNOSIS: Sponge oblong globular, firm, smooth, rounded lobate; fistules on upper surface, bifurcate, surmounted by oscula; fistules on under surface, rhizome-like; few oscula also flush with surface; ectosome microscopically hispid, with spongin crust 100-150 µm thick, containing uni- or pauci-spicular subsodictyal spicule tracts; choanosome with multispicular tracts, some vaguely ascending, and uni- or pauci-spicular tracts forming a disorganized subsodictyal reticulation; megascleres oxea, divided (arbitrarily) into two size ranges, 161-260 (204.44 µm, mean) long, 2-7 (4.1 µm) wide, 238-279 (255.8 µm) long, 7-11 (9.4 µm) wide; microscleres: toxa with reflexed tips, 8-82 (43.68 µm) chord length, 0.4-3.5 (1.66 µm) wide at widest point; sigmas, mostly centrangulate, 9-35 (18.76 µm) chord length, 0.5-2.0 (1.14 µm) wide.

DESCRIPTION OF HOLOTYPE: Sponge oblong-discoid, globular to lobate, 120×80×30 mm thick. Colour is light brown-beige in ethanol (Munsell 2.5Y8/4-lighter). Texture is firm, only slightly compressible, and moderately easily broken. Surface is smooth, optically even, with a few rounded lobes or bumps on upper surface, and several holes passing completely through the sponge; holes are 5-12 mm in diameter. Under-surface more convoluted, with rounded lobes and vermiform

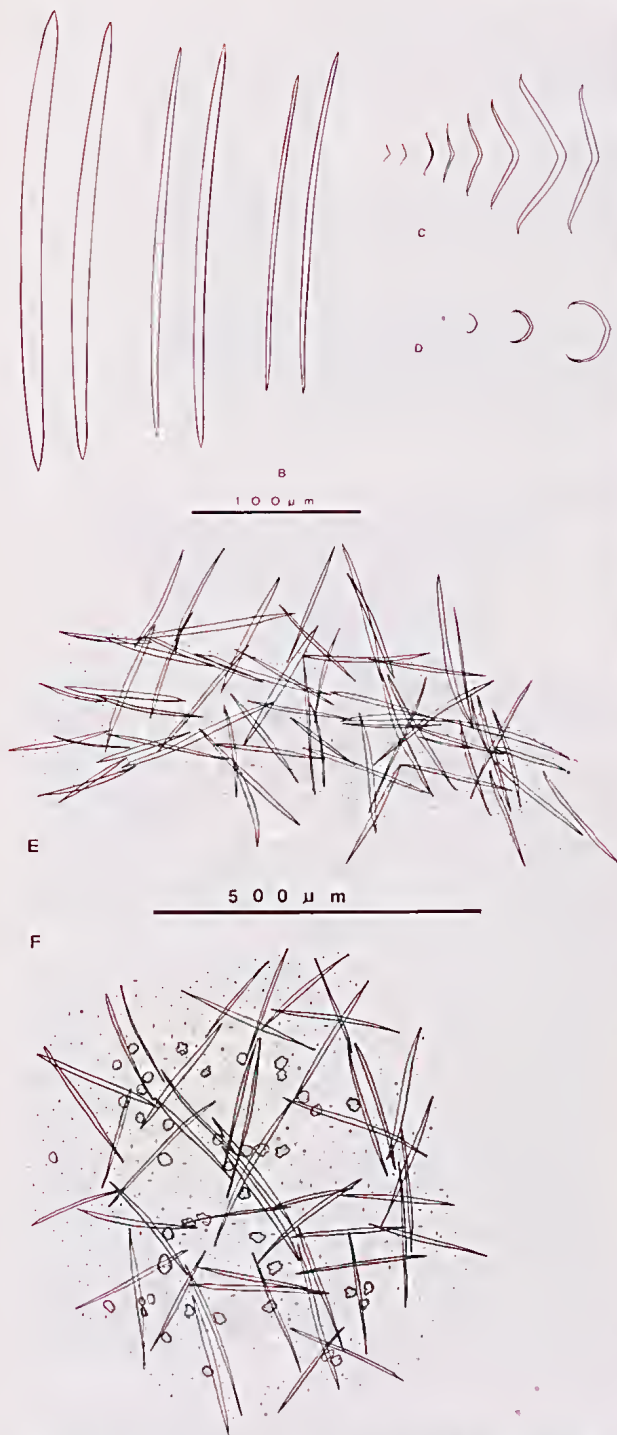


Fig. 1—*Biminia macrotoxa* sp. nov. skeletal components. A, large oxeas. B, smaller oxeas. C, toxas. D, sigmas; skeletal architecture, E, perpendicular section of peripheral skeleton. F, tangential view of ectosomal skeleton.

fistules. Remains of approximately 10 small fistules are present on upper surface, but few are entirely intact;



Fig. 2—*Biminia macrotoxa* sp. nov. Holotype NTMZ1478 (NMVF51373). 120 × 80 mm.

these are 6–10 mm long, 4–5.5 mm in diameter at base, 4–5 mm diameter at apex. Oscula are few, scattered over upper surface, fewer on underside; oscula measure 1.5–4.0 mm in diameter (flush with surface), and 3–4.5 mm in diameter on tips of fistules.

Ectosome is microscopically hispid, with tips of the ultimate spicules from choanosomal tracts poking through the ectosomal crust. The ectosome has a spongin crust, 100–150 μm thick, with a uni- or bispicular subsisodictyal surface reticulation. In cross-section, the tangential ectosomal skeleton appears to be mainly unispicular, and only occasionally bispicular, with tips of adjacent spicules overlapping slightly. Little to no spongin is present at spicule nodes, and if present, it is always loose (non-fibril) spongin. In transverse-section, the ectosomal skeleton can be seen as occasional meandering bispicular tracts, 20–40 μm wide, with numerous single spicules or uni-spicular tracts crossing at a vaguely triangular or rectangular isodictyal pattern. Subisodictyal architecture of the ectosomal skeleton is partially obscured by the projecting spicules of the choanosomal skeleton.

Spongin is granular, light brown in colour, occurring in ovoid bodies or as an amorphous conglomerate. Although spongin is mainly evenly distributed on ectosome, it is heavier in some regions, particularly at the base of fistules.

Choanosome is cavernous only below fistules, with cavities and canals measuring 150–550 μm in diameter, but is mostly densely packed with an irregular or subsisodictyal reticulation of (vaguely ascending)



Fig. 3—*Biminia macrotoxa* sp. nov. Paratype NTMZ1919 130×150 mm. Specimen cut in half. Upper portion shows under-surface; lower portion shows fistules on upper-surface.

multispicular tracts, 70–110 μm wide, consisting of 5–10 spicules abreast. Many multispicular tracts terminate at surface, with ultimate spicules projecting through ectosome. These are crossed by uni- or pauci-spicular tracts, 10–40 μm in width, or other non-ascending multispicular tracts, sometimes forming rectangular meshes, but mostly irregular and confused. Spicule tracts are thickest and most densely packed on inner surface of fistule walls, 80–150 μm thick, with up to 15 spicules abreast. Choanosomal spongin is mainly only visible around multispicular tracts, but patches of light spongin occur haphazardly throughout choanosome.

SKELETAL COMPONENTS (N=25): Megasccleres. Oxeas arbitrarily divided into two categories based on size; smaller variety fusiform, always sharply pointed, symmetrical, 204.44 μm long, 4.1 μm wide (mean), (range:

161–260×2–7 μm respectively); larger size category fusiform to hastate, sharply pointed, a few with slightly constricted or bluntly rounded ends, rarely with asymmetrical ends; 255.8 μm long, 9.4 μm wide (mean), (range: 238–279×7–11 μm respectively).

Microscleres. Toxas abundant, tricurvate, smooth mostly sharply bent at midsection, some rounded at bends, all with reflexed tips, variable size range; distributed throughout sponge, mostly associated with spongin; 43.68 μm chord length, 1.66 μm at widest point (mean), (range 8–82×0.4–3.5 μm respectively). Sigmas abundant, smooth, mostly centrangulate, few rounded C-shaped, variable size range; distribution as for toxas; 18.76 μm chord length, 1.14 μm at widest point (mean), (range 9–35×0.5–2.0 μm respectively).

DESCRIPTION OF PARATYPE: Sponge massive, lobate

TABLE 1
COMPARISON OF NEW AND KNOWN SPECIES OF *Biminia*
All measurements in micrometres unless otherwise indicated

	<i>B. macrotoxa</i> sp. nov.	<i>B. toxophila</i> (Dendy)	<i>B. stalagmitica</i> Wiedenmayer	<i>B. ooita</i> Hoshino
shape:	oblong, lobed	irregular, fusiform, tuberos	semi-encrusting base	spherical, massive
fistules:	bifurcate, on upper surface; rhizome-like on under surface; (6.60 × 4.8 mm)	2, tapering at each end (6.55 × 4 mm)	low or compound, some with oscula; rhizome-like fistules on under-surface (2.17 × 2.10 mm)	numerous, on upper surface only (20.40 × 6.8 mm)
surface:	smooth, lobed, even, microscopically hispid	uneven, irregular	smooth, velvety, microscopically hispid	smooth, even
texture:	firm, slightly compressible	rigid, brittle	tough, stiff	slightly compressible
ectosome:	100-150	'thin'	300-500	50-70
oxeas:	94-279 × 1.5-11	300 × 12	100-155 × 3.5-5	180-218 × 7-9
toxas:	8-82 × 0.4-3.5	57 or smaller	10-32 × 1	14-35 × 1
sigmas:	9-35 × 0.5-2	16.4	11-32 × 1	up to 45
source:	present study	Dendy, 1922, p. 45	Wiedenmayer, 1977, p. 124	Hoshino, 1981, p. 122
locality:	Timor Sea, Western Australia and Darwin, Northern Territory	Providence, Seychelles, Indian Ocean	Bimini, Western Bahamas	Ooita, Japan

base, 130 × 150 × 20-30 mm thick. Colour grey alive and in spirit (Munsell 5YR 7/2-lighter). Texture is compressible, easily broken. Surface as for holotype. Under-surface with several fistules, up to 60 mm long, 6 mm diameter, with terminal bifurcations, rhizome-like. Upper surface with numerous elongate hollow fistules, up to 60 mm long, 8 mm diameter, mostly with bifurcate tips, some surmounted by terminal oscula, others ending blindly; white alive, beige to grey in ethanol (5YR 8/2-lighter to 5YR 7/2).

Skeletal components (N=25). Megascleres: oxeas 166.9 µm long, 2.73 µm wide (mean) (range: 94-197 × 1.5-4 µm respectively); 201.05 µm long, 8.1 µm wide (171-230 × 6-10 µm respectively). Microscleres: toxas 31.45 µm chord length, 1.48 µm maximum width (11-63 × 0.5-3 µm respectively); sigmas 16.15 µm chord length, 1.4 µm maximum width (11-24 × 0.5-2 µm respectively).

ETYMOLOGY: The specific name refers to the relatively large toxon microscleire which is found in this species.

DISCUSSION: The genus *Biminia* was erected by Wiedenmayer (1977, p. 124) for two species, *Oceanapia toxophila* (Dendy 1922), the type-species, and *Biminia stalagmitica* Wiedenmayer. Both species have a spongin-enforced, tangential, ectosomal crust and fistules, typical of *Oceanapia* Norman species, but differ from that genus in having toxas as well as sigmas for microscleres. Wiedenmayer notes also that *Biminia* shows similarity to *Orina* Gray, in the haplosclerid family Haliclonidae (*sensu* Van Soest 1980) particularly in spiculation, but differs from *Orina*, and other

haliclonids, by the presence of blind fistules, a denser, more heterogeneous main skeleton lacking definite ascending spicule tracts, and a compound, often multilayered ectosomal crust (Wiedenmayer 1977, p. 125, Van Soest 1980, p. 85, 114). Hoshino (1981, p. 121) described a third species, *Biminia ooita* from Japan. All three species differ from *Biminia macrotoxa*, sp. nov. in most details of morphology and in skeletal measurements (Table 1). The validity of *Biminia* has been questioned by Van Soest (1980, p. 115), as he suggests that the presence of toxa may not be of sufficient importance to distinguish taxa at the generic level, and that *Biminia* is probably a junior synonym of *Oceanapia*. *Biminia* may be an artificial grouping but in practice offers a convenient basis for separation and differentiation of a large group of *Oceanapia*-like forms, one group with toxa (*Biminia*), the other without toxa (*Oceanapia*).

Family PETROSIIDAE Van Soest 1980

Acanthostrongylophora gen. nov.

DIAGNOSIS: Petrosiidae, with a lamellate-isotropic, heavily-meshed reticulation of spicule tracts cored by thick strongyles, and fewer, thin oxeas. Choanosome cavernous, spongin light, crumb-of-bread texture. Ectosome with an irregular subrectangular loose reticulation of megascleres. Microscleres microstrongyles, with minute microspines covering surface.

Acanthostrongylophora ashmorica sp. nov.

Figs 4, 5

MATERIAL EXAMINED: Holotype NMVF51374;

(NTMZ1495, Z.M.A. fragments of holotype) from north of Barracouta Shoals, Ashmore Reef, Timor Sea, Western Australia, lat. $12^{\circ} 18' 19''$ S, long. $124^{\circ} 04' 06''$ E; Coll. C. C. Lu, R.V. *Hai Kung*, station no. 70033105, trawl, 80-91 m depth, 31 Mar. 1981. Other Specimens: NTMZ1779 from west of Port Hedland, Western Australia, lat. $19^{\circ} 4.2'$ S, long. $118^{\circ} 54.0'$ E, coll. T. Ward, CSIRO R.V. *Soela* station no. 122, trawl, 82 m depth, 29 Aug. 1983; NTMZ1884 from west of Port Hedland, Western Australia, lat. $19^{\circ} 2.2'$ S, long. $118^{\circ} 4.1'$ E, coll. T. Ward, CSIRO R.V. *Soela* station

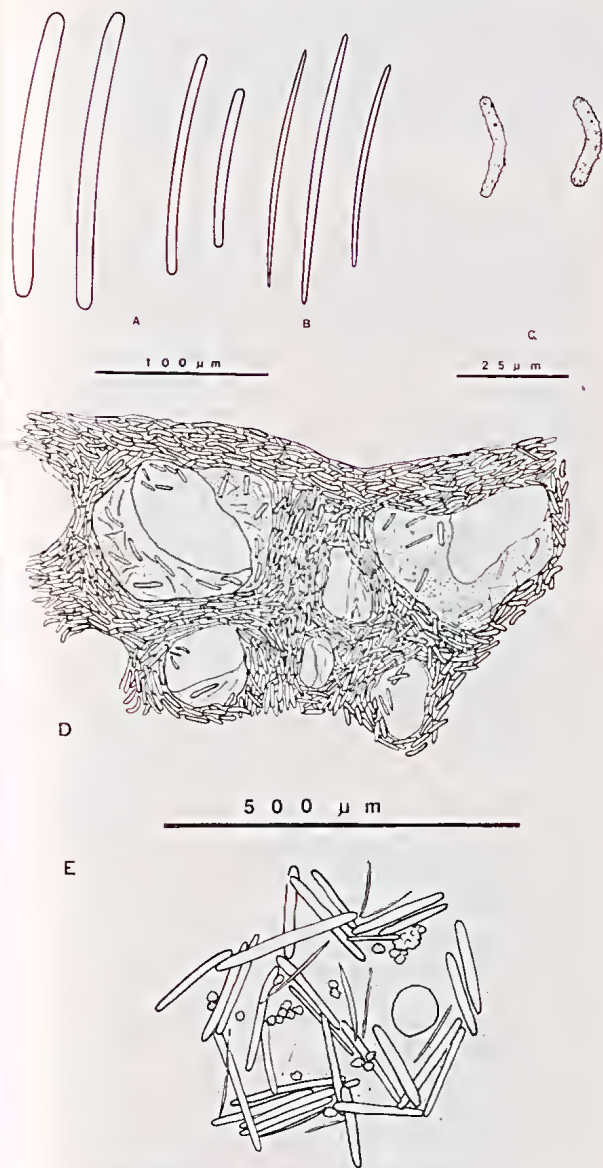


Fig. 4—*Acanthostrongylophora ashmorica* gen. et sp. nov. skeletal components. A, strongyles. B, oxeas. C, microstrongyles; skeletal architecture. D, perpendicular section of peripheral skeleton. E, tangential view of ectosomal skeleton.



Fig. 5—*Acanthostrongylophora ashmorica* gen. et sp. nov. Holotype NTMZ1495 (NMVF51374) 150 × 80 mm.

no. 136, trawl, 84 m depth, 1 Oct. 1983. (Both specimens fragmented).

DIAGNOSIS: Sponge massive, erect; firm, crumb-of-bread texture; sculptured, grooved surface; oscula large, flush with surface; thin transparent ectosome with subrectangular reticulation of loose megascleres and few microscleres; the choanosome is a heavily meshed reticulation of multispicular tracts, forming irregular ovoid meshes, halichondroid in places; megascleres are strongyles, 105-174 μ m (153.36 μ m, mean) long, 5-12 μ m (8.28 μ m) wide, and thin oxeas 98-173 μ m (139.56 μ m) long, 1-4 μ m (2.44 μ m) wide; microscleres are granular (minutely microspined) microstrongyles, 16-23 μ m (1.88 μ m) long, 1.5-4 μ m (3.08 μ m) wide.

DESCRIPTION OF HOLOTYPE: Sponge massive, elongate, oblong-cylindrical, probably erect (only portion of sponge was collected), measuring 150 × 80 × 90 mm at its widest. Colour is yellow-brown, slightly variegated, darker in grooves and ridges than on smoother areas of the surface (Munsell 5YR 3/4 to 2.5Y 8/4 in ethanol). Texture is firm to stony, barely compressible, but slightly brittle and relatively easy to crumble (and consequently difficult to section). In general, the consistency of the sponge resembles aggregated bread crumbs. The surface is shaggy, optically uneven, with a few large, deeply sculptured grooves and holes. Several large

oscula are present, not confined to any particular region of the surface, 7-15 mm in diameter.

Ectosome is thin, transparent (where it is intact), containing scattered pores, 40-65 μm in diameter, and an irregular, sub-rectangular reticulation of loose strongyles, interdispersed with oxeas and globular deposits of light spongin. The nodes of adjacent spicules are not connected by spongin; few microstrongyles are seen on the ectosome.

Spongin, where visible, is extremely light, occasionally granular, sometimes aggregated into ovoid bodies, and brown in colour.

Choanosome is cavernous in places, consisting of an irregular, heavy-meshed reticulation of thick spicule-tracts, 100-150 μm wide, fully cored by thick strongyles. Reticulation forms vaguely ovoid meshes, which are sometimes indiscernable from the halichondroid mass of single strongyles and oxeas which occur between many meshes. Mesh size ranges from 150 to 730 μm in diameter, sometimes containing light spongin, invariably containing loose megascleres, rarely microstrongyles.

SKELETAL COMPONENTS ($N=25$): Megascleres. Strongyles straight to symmetrically curved; variable in size and thickness; mostly evenly rounded, but some are strongyloxeote, with slightly tapering extremities; 153.36 μm long, 8.28 μm wide (mean), (range: 105-174 \times 5-12 μm respectively). Oxeas invariably thin, curved, mostly fusiform, sharp-pointed, some are hastate, approaching strongyloxeas, with slightly rounded or bluntly-pointed extremities; 139.56 μm long, 2.44 μm wide (mean), (range 98-173 \times 1-4 μm respectively).

Microscleres. Microstrongyles few, small, rounded extremities, slightly curved or straight; all with a granular appearance, produced by minute microspines covering the surface, resembling thick spirasters; 18.8 μm long, 3.08 μm wide (mean), (range: 16-23 \times 1.5-4 μm respectively).

DESCRIPTION OF OTHER SPECIMENS: Two specimens, both fragmented, formerly elongate to globular, approximately 60-80 \times 50-60 \times 40-60 mm at widest point. Colour as for holotype. Texture is barely compressible, but very easily crumbled. Surface is shaggy, crumb-of-bread.

SKELETAL COMPONENTS: Megascleres. Strongyles ($N=25$) 159.05 μm long, 9.65 μm wide (mean) (range: 130-177 \times 6-12 μm respectively). Oxeas ($N=25$) 133.7 μm long, 3.9 μm wide (79-170 \times 2-6 μm respectively). Microscleres. Microstrongyles rare ($N=10$) 18.8 μm long, 3.2 μm wide (17-23 \times 2-5 μm respectively).

ETYMOLOGY: This species is named for its first locality of collection, Ashmore Reef, Timor Sea.

DISCUSSION: *Acanthostrongylophora ashmorica* gen. et sp. nov. is closely related to the genus *Strongylophora* Dendy 1905, but differs in having acanthose microstrongyles. It also differs from other species of *Strongylophora*, except the type species of that genus, *S. durissima* Dendy 1905, in having a crumb-of-bread tex-

ture with a shaggy uneven surface. Apart from these characters, the present species may be differentiated from other members of *Strongylophora* as follows. *S. durissima* from Ceylon, Madagascar and Aldabra, has larger strongyles (260 \times 20 μm), and smaller oxeas (28 \times 2 μm); *S. strongylata* (Thiele 1903) from Indonesia, is digitate, has larger strongyles (325 \times 20 μm), and smaller oxeas (40 μm long); *S. dendyi* Hechtel 1969 from Barbados, is encrusting, has two distinct sizes of large strongyles (205 \times 7, 110 \times 5 μm respectively), and smaller oxeas (22 \times 1.5 μm); *S. davilai* Alcolado 1979 from Cuba, has small oxeas (30 μm long); and *S. hartmani* van Soest 1980 from Barbados, has larger strongyles (340 \times 34 μm), and two sizes of oxeas (252 \times 6, 91 \times 4 μm respectively). Van Soest (1980, p. 78, 136) provides a more detailed summary of the diagnostic characters for these species. Altogether *A. ashmorica* is most similar to *S. durissima*, which has an Indian Ocean distribution.

ACKNOWLEDGEMENTS

I wish to thank Dr C. C. Lu, Curator, Department of Invertebrate Zoology, Museum of Victoria, for access to the Porifera collection at the Museum, Dr T. Ward for 'Soela' material, and Dr R. W. M. Van Soest and Dr F. Wiedenmayer for their comments on the manuscript.

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REDEFINITION OF *MUNNA* AND *UROMUNNA*
(CRUSTACEA: ISOPODA: MUNNIDAE), WITH
DESCRIPTIONS OF FIVE SPECIES FROM COASTAL
VICTORIA

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ABSTRACT: The subgenera *Munna* and *Uromunna* (two of five in the genus *Munna*) are elevated to generic rank on the basis of already-known and additional characters. The subgenus *Neomunna* is synonymised with *Munna*; the subgenus *Pangamunna* and the genus *Munnoides* are synonymised with *Uromunna*; and the subgenus *Metamunna* (preoccupied) remains in doubt. Five species of *Munna* and *Uromunna*, four new, the first recorded from eastern Australia, are described from coastal Victoria: *U. brevicornis* (Thomson) from seagrass in estuarine Gippsland Lakes; *M. hovelli* and *U. phillipi* from shallow benthos of Port Phillip Bay; *M. hentyi* and *U. humei* from intertidal rocky shores on Bass Strait. *Uromunna phillipi* is also recorded from eastern Tasmania. A list of species of *Munna* and *Uromunna* is appended.

The asellote isopod family Munnidae was recently confined to only four genera (*Munna* Krøyer, *Astrurus* Beddard, *Echinomunna* Vanhöffen and *Zoromunna* Menzies & George). Most of the known species have been assigned to *Munna*, the relationships of the smaller genera to *Munna* are not clear and the composition of the family somewhat uncertain (Wilson 1980). The position is further complicated by other available genus-group names: *Haliacris* Pfeffer 1887, and *Caecimunna* Richardson 1908 (usually taken to be junior synonyms of *Munna*); *Munnoides* Carvacho 1977, and five subgenera of *Munna*—*Munna*, *Uromunna* and *Neomunna* (Menzies 1962), *Metamunna* (Fresi & Mazzella 1974) and *Pangamunna* (Schultz 1979). In this contribution the systematics of the subgenera of *Munna* and the genus *Munnoides* are examined and a new generic arrangement proposed. The study is based on five new Australian species, dissection of several representatives of each of the subgenera, and examination of descriptions and figures of the remaining species known.

GENERA OF THE MUNNIDAE

Wilson (1980) discussed but left unresolved the status of *Astrurus*, *Echinomunna*, *Zoromunna*, *Haliacris* and his new genus A; this contribution adds nothing to his comments but I agree with him that 'revision of the taxon *Munna* will yield several more genera'. These will not be based on the existing subgenera which I discuss below.

Dissection of specimens of *Munna* (*Neomunna*) *kroyeri* and examination of written descriptions and figures of numerous other species of *Neomunna* lead me to believe that this subgenus and *Munna* are synonymous. The presence or absence of a hook on the uropod is the only distinguishing character but it can no longer be considered of even subgeneric value. In many species (e.g., *M. boeckii*, *M. halei*, *M. lundae*, *M. maculata*, *M. urupica*) truncate or cassellate uropods are found. These tend to grade into those species previously

assigned to *Neomunna* in which the uropodal hooks are poorly developed.

The subgenus *Metamunna* seems unrelated to any of the other subgenera because of the single dactyl on pereopods 2-7. It therefore requires further investigation. Incidentally, the name *Metamunna* Fresi & Mazzella 1974, is preoccupied by *Metamunna* Tattersall, a genus probably referable to the Pleurogoniidae (Tattersall 1906). Barnard (1920) synonymised *Metamunna* Tattersall with *Paramunna* Sars, a move supported by Nordenstam (1933) and Kussakin (1967). The subgenus is not considered further here.

The subgenera *Uromunna* and *Munna* are more clearly differentiated. *Uromunna* was originally diagnosed by Menzies (1962) as possessing 'leaf-like ventral uropodal ramus flattened in cross-section. Apical spines lacking'. In contrast, the subgenus *Munna* possesses 'inferior uropodal ramus rounded in cross-section, lacking recurved apical spines'. To these characters have been added: antenna I (Kussakin 1962), male pleopod 1, pleopod 3, and pereopod 1 (Frankenberg & Menzies 1966) and mandibular palp (Fresi & Mazzella 1974).

Most authors (Fresi & Mazzella 1974, Kensley 1980) agree that the shape of the uropodal ramus is a character of little value but that the separation of these two groups still has value. The five Australian species support this. My examination of type species, *M. (Munna) boeckii* Krøyer and *M. (Uromunna) ubiquita* Menzies, and of published descriptions of more than 60 other species justifies elevation of the subgenera *Munna* and *Uromunna* to generic rank.

Most of the characters used to separate the two genera are not new. However, the presence of integumental setae and spines, molar setae, and serrate spines on the mandibular palp in *Munna* and sexual dimorphism in pereopod 2 of *Uromunna* are newly reported. Overall, *Uromunna* has more advanced characters: a single aesthetasc, shortened mandibular palp, sexual dimorphism in pereopod 2 and absence of a distolateral projection bearing a groove on pleopod 1. In addition, some species of *Uromunna* are estuarine; all

species of *Munna* are truly marine. *Munna*'s only advanced feature is the sexual dimorphism of pereopod 1, best seen in Australian species in *M. hentyi*. There are indications that the two genera are biogeographically distinct which further supports their separation.

The genus *Munna* remains rather large and diverse (see Appendix). Wilson (1980) suggested that the generic name *Haliacris* Pfeffer might be appropriate for those species which have a huge pereopod 1 in the male and very long legs and antennae. No such division is readily apparent from examination of numerous species descriptions. Adult males of so few species have been described that allocation of species to *Haliacris* and *Munna* is not appropriate at this stage. *Munna* appears confined to cool temperate and polar seas, the Southern Ocean, southern Australia and New Zealand, southern South America, the northern Pacific, North Atlantic and Arctic Sea. Exceptions to this are records from California (northern part only) and from the Mediterranean. The largest numbers of reported species are from the north-western Pacific (Kussakin 1962, 1972) and from islands of the Southern Ocean (Kussakin 1967). Several undescribed species are known to me from throughout Australia and the New Zealand subantarctic.

The genus *Uromunna* is smaller, with only 15 species (see Appendix). Five of these lack mandibular palps and have been placed in a separate genus (*Munnoides*) or subgenus (*Pangamunna*) herein considered junior synonyms of *Uromunna*. Diagnoses of the two are indistinguishable and I refer to this group of species as '*Munnoides*'. Loss of mandibular palps is a frequent phenomenon in janiroid isopods and considerable evidence suggests that this alone is not a useful systematic character. Species of '*Munnoides*' display no other unique advanced character and their apparent sister-group, palpate species of *Uromunna*, themselves show no unique features. All species of '*Munnoides*' are estuarine, some extending into fresh water, and most are warm temperate or tropical but this apparent homogeneity is contradicted by their wide geographic distribution. Also, estuarine species of palpate *Uromunna* are known (*U. schauinslandi* and *U. brevicornis*) as are tropical species (*U. acarina*). I suspect that a loss of mandibular palp occurred several times in estuarine or tropical *Uromunna* stock.

A further loss of mandibular palps occurred in Wilson's (1980) genus A in the southern Atlantic deep sea, this time apparently from *Munna* stock. In addition, two pleurogoniid genera have been defined on the basis of absence of mandibular palp. *Munnogonium* George & Strömberg is separated from *Austrosignum* Hodgson in this way (Bowman & Schultz 1974, Wilson 1980) as is *Coulmannia* Hodgson from *Nofoxenoides* Menzies (Wilson 1980). In neither case is the separation supported by other unique character states and the palpate genera show no unique advanced features. I believe that loss of the mandibular palp, in munnids and pleurogoniids at least, is a common, independently and frequently derived phenomenon like loss of eyes in the deep sea (Wolff 1962).

In contrast to *Munna*, the genus *Uromunna* is found in temperate and tropical seas, as well as in cooler Southern Hemisphere waters. The genus is absent from cold Northern Hemisphere seas where many species of *Munna* are known.

AUSTRALIAN ASELLOTA

The asellote isopod fauna of Australia is almost totally unknown. Exceptions are four species of the genus *Stenetrium* (Nicholls 1929), one species of *Munna* from Western Australia (Thomson 1946), two incompletely described species of *Munnopsis* and *Ilyarachna* (Monod 1973), and *Prethura*, a new genus of Pleurocopidae from Queensland (Kensley 1982). The Munnidae is widespread in coastal habitats and it is not surprising that it is well represented by species in Australia. In this contribution five species from the collections of the Museum of Victoria, formerly the National Museum of Victoria (NMV), are described, and a key to separate them is presented.

Some material for this study has come from environmental surveys by the Victorian Ministry for Conservation: the Gippsland Regional Environmental Study, 1978-9 (GRES) and the Port Phillip Bay Environmental Study, 1969-73 (PPBES). Figures of limbs are drawn from permanent slides using polyvinyl lactophenol mountant. Scale lines are 0.1 mm unless marked otherwise.

Abbreviations on figures are as follows: A1, 2, antennae 1, 2; MD, mandible; MP, maxilliped; MX1, 2, maxillae 1, 2; P1-P7, pereopods 1-7; PL1-4, pleopods 1-4; PT, pleotelson; O, operculum (pleopod 2 of female); U, uropod.

KEY TO AUSTRALIAN SPECIES OF MUNNA AND UROMUNNA

1. Pereon dorsally setose. Pereopod 1 sexually dimorphic, more developed in male. Antenna 1 with 2 aesthetascs, its last article minute. Mandibular palp reaching beyond end of incisor. Male pleopod 1 with acute distolateral projections. Pleopods 3 exopod of similar width to endopod *Munna* 2
- Pereon dorsally with few if any setae. Pereopod 1 of both sexes similar. Antenna 1 with 1 aesthetasc, its last article not minute. Mandibular palp not reaching to end of incisor. Male pleopod 1 simple, without distolateral projections. Pleopod 3 exopod much narrower than endopod *Uromunna* 3
2. Dorsal setae in transverse rows of 10-20 per pereonite. Anterior margin of head bearing strong spines. Antenna 2 flagellum articles as long as wide. Male pereopods 1 massive, carpocheate .. *M. hentyi*
- Dorsal setae scattered, less than 10 per pereonite. Anterior margin of head bearing setae only, no spines. Antenna 2 flagellate articles elongate. Male pereopods 1 subchelate *M. hovelli*
3. Pereopod 1 palm with minute spines. Eyes large, diameter about $\frac{1}{4}$ of head width. Estuarine *U. brevicornis*



Fig. 1—*Munna hentyi*. Male, 1.81 mm, NMVJ1083; a, female, 1.62 mm, NMVJ1082.

- Pereopod 1 palm without minute spines. Eyes small, diameter about $\frac{1}{5}$ of head width. Marine 4
- 4. Head as long as 2 pereonites. Dactyls of pereopod 2 six times as long as wide, unguis very fine . *U. phillipi*
- Head as long as 4 pereonites. Dactyls of pereopod 2 three times as long as wide, unguis stout . . . *U. humei*

SYSTEMATICS

Genus *Munna* Krøyer 1839

- 1839 *Munna* Krøyer, p. 612.
- 1887 *Haliacris* Pfeffer, p. 137.
- 1908 *Caecimunna* Richardson, p. 79.
- 1962 *Munna* (*Munna*) Menzies, p. 32.
- 1962 *Munna* (*Neomunna*) Menzies, p. 36.

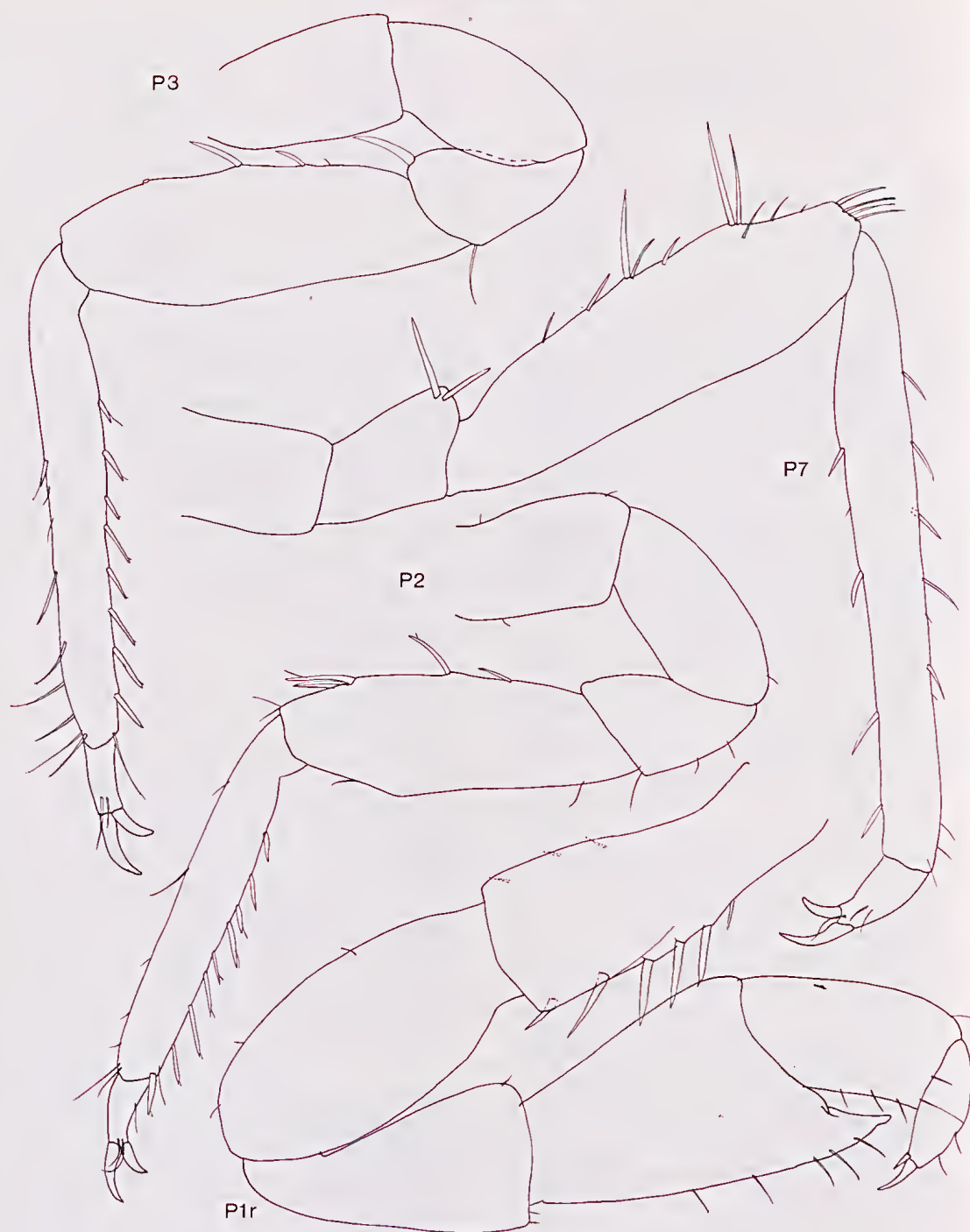


Fig. 2—*Munna hentyi*. Male, 1.81 mm, NMVJ1083 (r = right).

DIAGNOSIS: Munnidae with numerous dorsal setae and often with articulating spines on head, pleon and pleopods 1 and 2. Antenna 1 with last article of flagellum minute, it and the penultimate article each with a single aesthetasc. Mandibular molar strong and subcylindrical, its surface truncate, and bearing ac-

cessory setae; palp reaching beyond the end of the incisor, its second article bearing 1-2 serrate spines. Maxillipedal epipod with an acute apex. Pereopod 1 sexually dimorphic, in male sometimes enlarged, often massively, sometimes carpocheate. Pereopods 2-7 not (or barely) sexually dimorphic; dactyls with accessory

claws. Pleopod 1 of male with a more or less acute (often markedly projecting) distolateral angle bearing grooves. Pleopod 3 exopod with a broad second article reaching well beyond the endopod.

TYPE SPECIES (by monotypy): *Munna boeckii* Krøyer 1839.

SPECIES INCLUDED: See Appendix.

Munna hentyi sp. nov.

Figs 1-3

MATERIAL EXAMINED: *Holotype*: female, 1.96 mm, NMVJ1077. Vic., Apollo Bay (38°45'S., 143°41'E.), from *Macrocystis* holdfasts, W. F. Seed, 28 Dec 1970. *Paratypes*: Vic., type locality, NMVJ1078-80 (4 females, 2 juvenile males, 1.4-1.8 mm). Grassy Creek, 7 km N. of Lorne (38°29'S., 144°02'E.) from small rock pool, W. F. Seed, 23 Jan 1968, NMVJ1081-3 (6 females, 1 adult male, 0.9-1.8 mm). Aireys Inlet, W. F. Seed, 29 Jan 1968, NMVJ1084 (1 male, 1.0 mm).

DESCRIPTION: *Male*. First five pereonites only slightly increasing in width posteriorly, but pereonite 1 with more developed shoulders than following pereonites. Head only little narrower than pereonite 1; anterior margin concave, with row of 8-10 spines, upper lip projecting; eyelobes with anterior subterminal projection. Pleon with free first pleonite as long as pereonites; pleotelson globose, 1.5 times as long as wide. Integument with scattered brown pigment dorsally, pereon and pleotelson with transverse rows of dorsal setae.

Antenna 1 with 2 broad basal articles, 2 short narrow articles, and 3 narrow articles, last minute; last two each bear a single aesthetasc. Antenna 2 peduncle of 3 short broad articles and 2 elongate articles; flagellum of 25 articles, as long as rest of peduncle; total antenna as long as body. Mandible with 3-articled palp reaching well beyond incisor; article 1 with 1 simple seta, article 2 with 2 pectinate and 1 simple setae, article 3 with 4 fringed setae; incisor with 4-5 cusps; lacinia mobilis on one side only, with 4 teeth; spine row of 4 serrate spines; molar process prominent, with complex toothed grinding surface bearing 2 lateral setae. Maxilla 1 inner ramus with 4 spines, outer ramus with 10 spines plus setae. Maxilla 2 rami with distal simple and complex setae, extending mesially along inner ramus. Maxillipedal epipod almost triangular, reaching second palp article; endite with 6 distal spines, 5 submarginal lanceolate blades, 7 spines distomesially and 2-3 retinaculæ; palp of 5 articles, first four with 1, 8, 8 and 8 setae mesially, last article with 5 setae and 2 terminal spines.

Pereopods 1 asymmetrical in only adult known. Left pereopod 1 grossly enlarged, carpocheate; article 2 with 8 spines along anterior margin; article 3 swollen; article 4 distally enlarged; article 5 swollen, with distal complex thumb bearing scattered setae; article 6 only half as long as 5, with distal recurved thumb, setose; dactyl a curved dagger closing on article 5, setose, unguis about one-fifth length of dactyl. Right pereopod 1 about two-thirds size of left, similar in general form but less swollen,

notably article 6 is without distal thumb and unguis is relatively larger. Pereopods 1 symmetrical and smaller in juvenile males, similar in form to smaller pereopod of adult but differing in article 5 having 3 stout spines on triangular thumb, article 6 more rounded distally. Pereopods 2-7 increasing in length posteriorly, with more spines posteriorly. Pereopod 2 article 4 with 2 long anterodistal spines; article 5 with 1+2+2 anterior spines; article 6 is 6 times as long as wide, with 9 spines along posterior margin; dactyl with fine unguis two-thirds as long as rest of dactyl, and shorter supplementary claw. Pereopod 3 similar to 2 but more elongate. Pereopod 7 article 5 with spinose anterior margin; article 6 is 9 times as long as wide, with spines on anterior and posterior margins; dactyl with fine unguis, half as long as rest of dactyl, and smaller supplementary claw.

Pleopod 1 with strong lateral projections each with 2 setae near the apex, apical margin rounded mesially and bearing 5 setae distolaterally. Pleopod 2 apex narrowly rounded, bearing 6 submarginal setae. Pleopod 3 endopod with 3 stout terminal setae; exopod broader and longer than endopod, of 2 articles, second with 6 submarginal setae. Pleopod 4 endopod subacute, exopod of 2 articles with 2 long terminal setae.

Uropod without peduncle, lower ramus with about 6 setae; upper ramus minute and with 1 seta.

Female. Pereonites 3 and 4 widest, pereonite 1 without developed shoulders. Head as in male but spines may cover a triangular area near anterior margin. Pereon with transverse rows of setae, pleotelson with 5-6 spines laterally.

Antennae and mouthparts as in male.

Pereopods 1 smaller than other limbs, symmetrical. Pereopod 1 article 4 with 2 anterodistal spines and 1 posterodistal spine; article 5 with broad posterior lobe bearing 5 spines, with 1 anterior spine; article 6 with convex palm minutely spinose along its distal section, 2 mesial and 3 anterior spines; dactyl minutely spinose, unguis two-thirds length of rest of dactyl and with a substantial supplementary claw. Pereopods 2-7 as in male.

Pleopod 2 about as wide as long, bearing numerous setae including 16 submarginally. Pleopods 3-5 as in male.

Uropod as in male.

ETYMOLOGY: *Munna hentyi* is named for Edward Henty (1810-1878) who, in 1834 in Portland, became the first permanent settler in Victoria.

REMARKS: *Munna hentyi* is the only species so far known from Australia in which the male possesses a massive carpocheate first pereopod. In the larger male figured, the first pereopods are decidedly asymmetrical but in the smaller male only marginally so. Massive carpocheate first pereopods are common in species of *Munna*, particularly in the Southern Hemisphere (e.g., *M. neozelanica*, *M. antarctica* and *M. neglecta* (Nordenstam 1933)). Of these, *M. hentyi* most resembles *M. neglecta*. The male first pereopods are similar and both species have a transverse row of spines on the head.

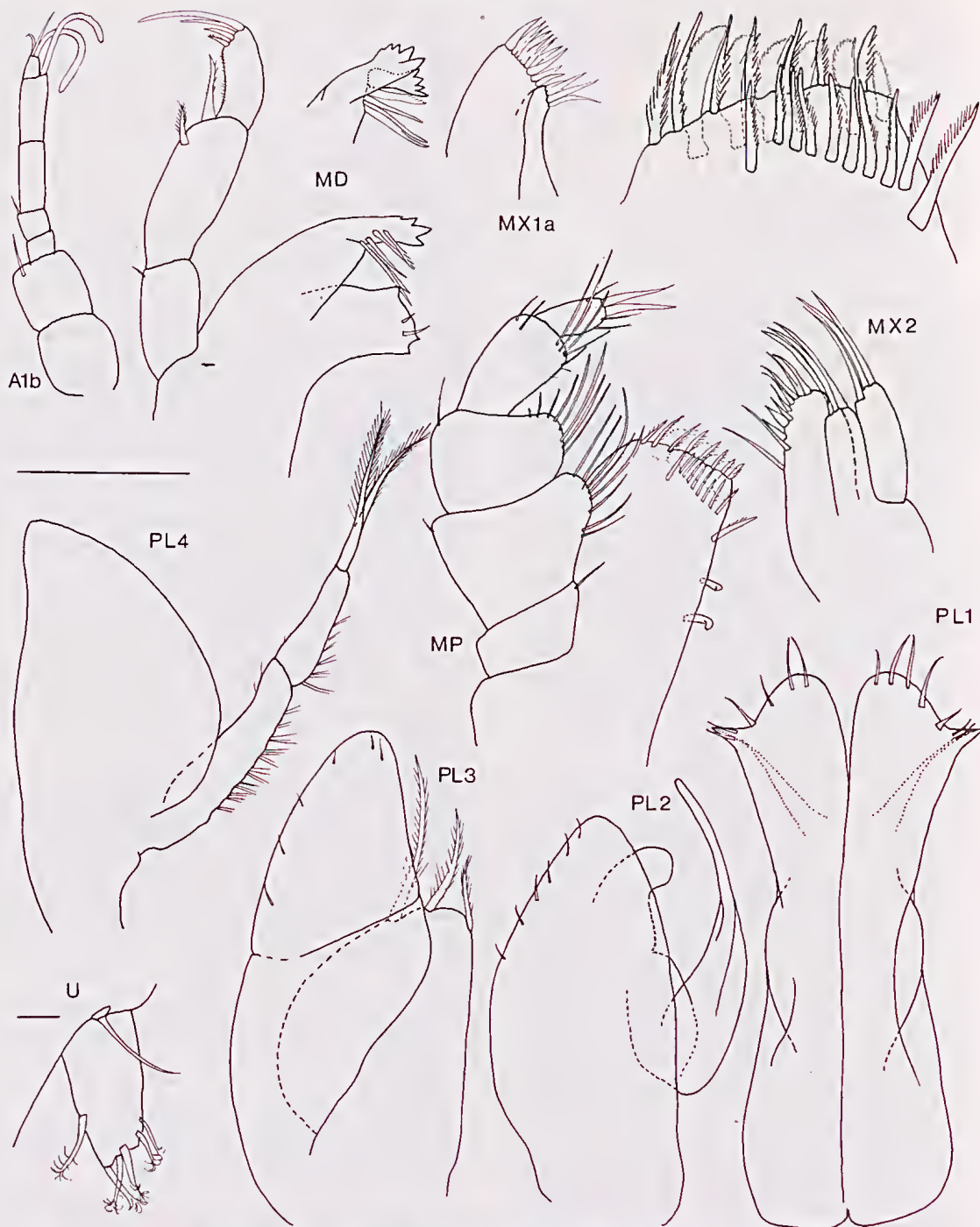


Fig. 3—*Munna hentyi*. Male, 1.81 mm, NMVJ1083; a, female, 1.68 mm, NMVJ1082.; b, male, 1.57 mm, NMVJ1080.

***Munna hovelli* sp. nov.**

Figs 4-6

MATERIAL EXAMINED: *Holotype*: female, 1.74 mm, NMVJ1063. Vic., Port Phillip Bay, off Werribee sewage-treatment farm 145W drain, (38°00'S.,

144°36'E.), shelly-sand, 5 m, G. Poore, 18 Nov 1975. *Paratypes*: Vic., type locality, NMVJ1064 (1 male, 1.6 mm) NMVJ1065-7 (6 females, 1.3-1.9 mm). Hobsons Bay, Generator Beacon, artificial substrates, 1 m, N. Holmes, 9 Feb 1976, NMVJ1068 (1 female, 1.66 mm). Hobsons Bay, Breakwater Pier, artificial



Fig. 4—*Munna hovelli*. Female, 1.64 mm, NMVJ1066; a, female, 1.75 mm, NMVJ1072; b, female, 1.74 mm, NMVJ1063.

substrates, 1 m, N. Holmes, 25 Aug 1975, NMVJ1071 (1 male, 1.66 mm), NMVJ1072 (1 female, 1.75 mm).

DESCRIPTION: Female. Body half as wide as long. Pereonites 3 and 4 the widest. Head wider than pereonite 1; anterior margin straight, with submarginal

row of about 12 setae, upper lip projecting well in front of head. Pleon with free first pleonite; pleotelson globose, 1.3 times as long as wide. Integument of pereon with transverse rows of setae, pleon with scattered dorsal setae.

Antenna 1 with 2 broad basal articles, 2 short narrow

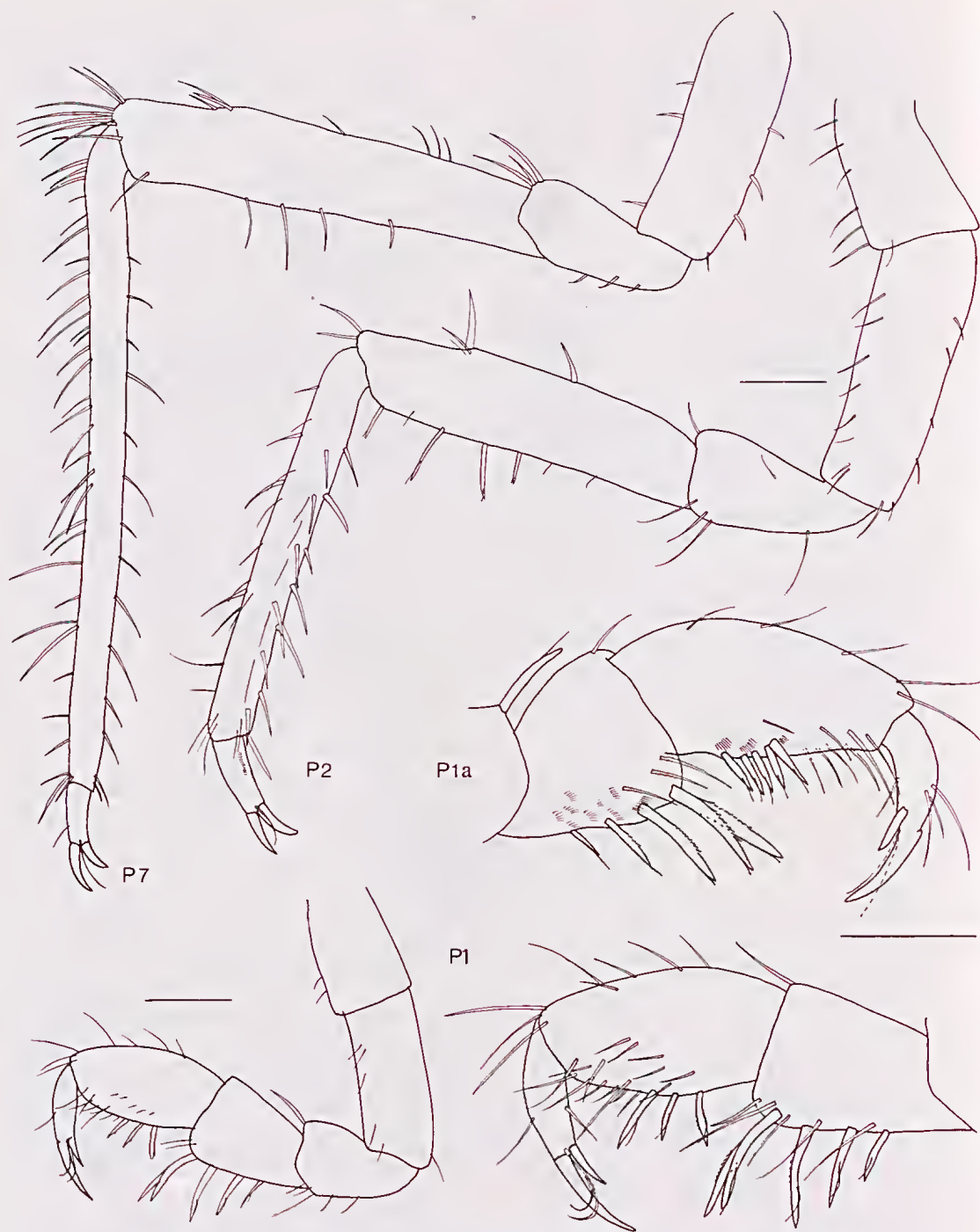


Fig. 5—*Munna hovelli*. Female, 1.85 mm, NMVJ1067; a, male, 1.66 mm, NMVJ1071.

articles, plus 1 long and 1 minute article, each bearing single aesthetasc. Antenna 2 peduncle of 3 short basal articles plus 2 extremely elongate articles; flagellum of 12 articles, about as long as last 2 articles of peduncle; total antenna 1.7 times length of body. Mandible with 3-articled palp reaching beyond incisor; article 1 with

single seta, article 2 with 2 serrate setae, article 3 with 3 terminal serrate setae; incisor with 4 cusps; Lacinia mobilis on one side only, with 4 teeth; spine row of 4-5 spines; molar process tuberculate and with lateral spine. Maxillae typical of genus. Maxillipedal epipods subtriangular, reaching to third palp article; endite with 5

distal spines, 4 submarginal fan-shaped setae, 5 spines distomesially and 3-4 retinaculæ; palp of 5 articles, first four with 1, 7, 9 and 5 setae mesially, last article with 3 setae and 2 terminal spines.

Pereopods 1 symmetrical, much smaller than more posterior limbs. Pereopod 1 article 5 with 5 long posterodistal spines; article 6 palm barely convex, setose, with 3 spines on margin; dactyl bearing fine unguis equal to 0.4 its length, supplementary claw acute. Pereopods 2-7 increasing in length posteriorly, more spinose posteriorly. Pereopod 2 article 5 with 4 spines on posterior margin; article 6 is 9 times as long as wide, densely spinose; dactyl with unguis only half as long as rest of dactyl, supplementary claw as long as unguis. Pereopod 7 article 5 with 4 spines posteriorly, grouped spines anteriorly; article 6 is 20 times as long as wide,

densely spinose; dactyl with short unguis and shorter supplementary claw.

Pleopod 2 subcircular, setose except near midline; 4-10 stout spines proximally. Pleopod 3 endopod with 3 stout terminal setae; exopod broader and longer than endopod, of 2 articles, the second with 4-7 submarginal setae. Pleopod 4 exopod of 2 articles with 2 long apical setae.

Uropod without peduncle; lower ramus 3 times as long as wide; upper ramus minute, with single long seta.

Male. Head, pereon and pleon as in female.

Pereopod 1 more developed than in female, article 5 with 6 posterior spines; article 6 palm straight, with 5 spines on mesial face; dactyl with fine unguis equal to half its length, supplementary spine acute. Pereopods 2-7 as in female.

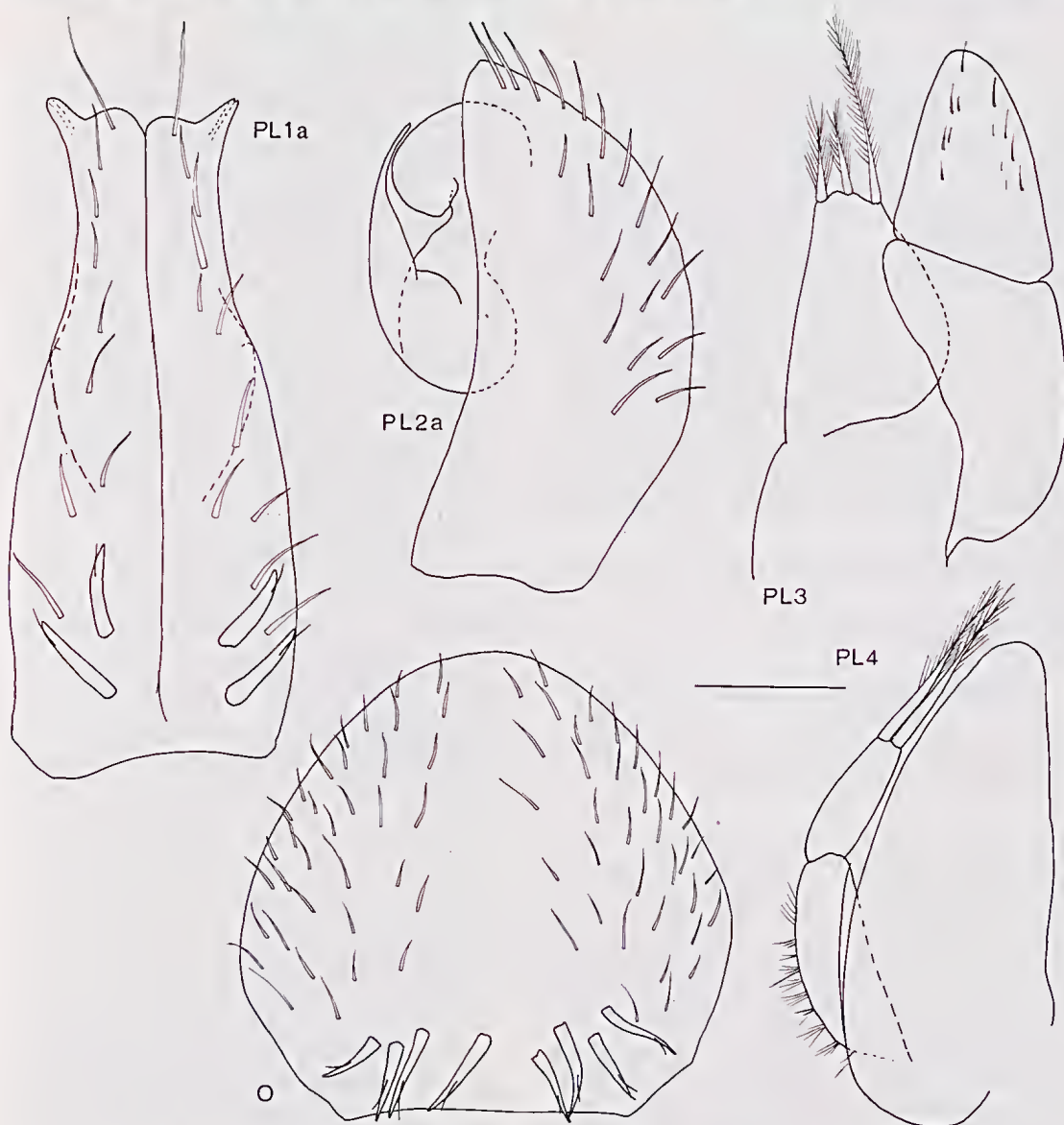


Fig. 6—*Munna hovelli*. Female, 1.85 mm, NMVJ1067; a, male, 1.66 mm, NMVJ1071.

Pleopod 1 with strong distolateral projections, about 10 setae along each side and 2 pairs of setae proximally. Pleopod 2 broad, ventrally setose.

ETYMOLOGY: *Munna hovelli* is named for William Hilton Hovell (1786-1875) who, in 1824 with Hamilton Hume, lead an expedition from Sydney and reached Port Phillip Bay.

REMARKS: *Munna hovelli* is distinguished from other Australian species by the setose dorsal integument coupled with only moderate development of the subchelate first pereopod of the male. There is a real possibility that both males examined were immature. Few species of *Munna* lack a well-developed carpo-chelate male first pereopod but two species, *M. chilensis* and *M. lundae* (Menzies, 1962), apparently lack any sexual dimorphism in this limb.

Genus *Uromunna* Menzies 1962

1962 *Munna (Uromunna)* Menzies, p. 36.

1977 *Munnoides* Carvacho, p. 6.

1979 *Munna (Pangamunna)* Schultz, p. 577.

DIAGNOSIS: Munnidae with few of any dorsal setae, without dorsal articulating spines. Antenna 1 last article not minute, bearing single aesthetasc. Mandibular molar strong and subcylindrical, its truncate surface without accessory setae; palp not reaching to end of incisor, its second article without spines, or palp absent. Maxillipedal epipod oval. Pereopod 1 not sexually dimorphic, symmetrical, small. Pereopod 2 (rarely 2-7) sexually dimorphic, articles 5 and 6 of male broader than those of female; dactyls with accessory claws. Pleopod 1 of male simple, without distolateral projections, grooves terminating at or near truncate distal margin. Pleopod 3 exopod with a narrow second article barely reaching beyond endopod.

TYPE SPECIES: *Munna ubiquita* Menzies, 1952 (original designation).

SPECIES INCLUDED: See Appendix.

Uromunna brevicornis (Thomson 1946)

Figs 7-9

1946 *Munna brevicornis* Thomson, p. 50, fig. 5.

1982 *Munna brevicornis* Thomson; Poore, p. 909.

MATERIAL EXAMINED: Vic., Gippsland Lakes, Fraser Island (38°16.4'S., 147°33.3'E.), seagrass on sand, 1 m, 26 Mar. 1979 (GRES station 3073): NMVJ1054-7, J1059-62 (14 males, 1.0-1.3 mm; 25 females, 1.0-1.4 mm), NMVJ1047 (100+ specimens). Same locality, 30 Nov. 1978, NMVJ1048 (36). Same locality, 31 May. 1979, AM P32256 (36). Gippsland Lakes, Banksia Peninsula, seagrass on sand, 1 m, 29 Mar. 1979 (GRES station 3072), NMVJ1049(1). Same locality, 2 Nov. 1979, NMVJ1050(17). Gippsland Lakes, SW. end of Lake Victoria (GRES station 3071), 2 Nov. 1979, NMVJ1051(9). Gippsland Lakes, Resides Jetty, 31 May 1979, NMVJ1052(4). Same locality, 1 Mar. 1979,

NMVJ1053(11). Sydenham Inlet, S. McCallum, Jan. 1979, NMVJ1058(15).

TYPE LOCALITY: WA., Freshwater Bay, Swan River, on algae.

DESCRIPTION: *Male.* Body 2.5 times as long as wide. First five pereonites more or less same width but pereonite 1 with more developed shoulders than pereonite 2. Head only little narrower than pereonite 1; anterior margin straight, upper lip distinct and projecting in front of head. Pleon with single free first pleonite; pleotelson globose, 1.3 times as long as wide. Integument largely without dorsal setae; with diffuse red-brown pigment dorsally, more pronounced as a pair of longitudinal stripes running from behind the eyes to the edges of pleonite 1.

Antenna 1 with 2 broad basal articles, 2 short and narrow articles, and 2 tapering elongate articles of which the second is little shorter than first; single aesthetasc on the terminal article. Antenna 2 peduncle of 3 short basal articles and 2 elongate articles; flagellum of 14 articles, little longer than peduncle; total antenna about as long as body. Mandible with 3-articled palp not reaching to end of incisor, first article with 1 seta, last article with 2 terminal setae; incisor of 4 cusps; lacinia mobilis on one side only, with 4 teeth; spine row of 3-4 serrate spines; molar process prominent, with tuberculate grinding surface and without setae. Maxilla 1 inner ramus with 4 spines and outer ramus with 11 spines. Maxilla 2 rami with distal simple and complex setae, extending mesially along inner ramus. Maxillipedal epipod oval, reaching second palp article; endite with 4 distal spines, 3 sub-terminal lanceolate spines, 2-3 setae near mesial margin and 3 retinaculae; palp of 5 articles, first four with 1, 3, 3 and 3 setae mesially, last article with 4 setae and 2 terminal spines.

Pereopods 1 symmetrical, shorter than following legs; article 4 with anterodistal spine; article 5 with 3 long posterodistal spines; article 6 with convex palm bearing row of 30-35 minute closely-set spines along most of length and 3 long acute spines on mesial face; dactyl with 1 long spine at base of unguis; unguis one-third of length of dactyl. Pereopods 2-7 increasing in length posteriorly. Pereopod 2 article 4 with long anterodistal spine; article 5 widest one-third way along, with 4 closely spaced setae proximally and 3 spines distally on posterior margin; article 6 with 5 spines along distal two-thirds of posterior margin; dactyl with fine unguis as long as rest of dactyl, and short stout supplementary claw. Pereopod 3 similar, but more elongate than pereopod 2. Pereopod 7 article 5 with 4 fine spines on posterior margin and 2 groups of 3 spines on anterodistal margin; article 6 is 15 times as long as wide, with fine spines; dactyl with fine unguis, a little shorter than rest of dactyl, and substantial supplementary claw.

Pleopod 1 strongly curving laterally at tip, each apex rounded with 2 pairs of setae along free mesial margin. Pleopod 2 apex oblique, bearing 4 terminal setae. Pleopod 3 endopod with 2 long stout plumose setae; exopod much narrower, of 2 articles, both marginally

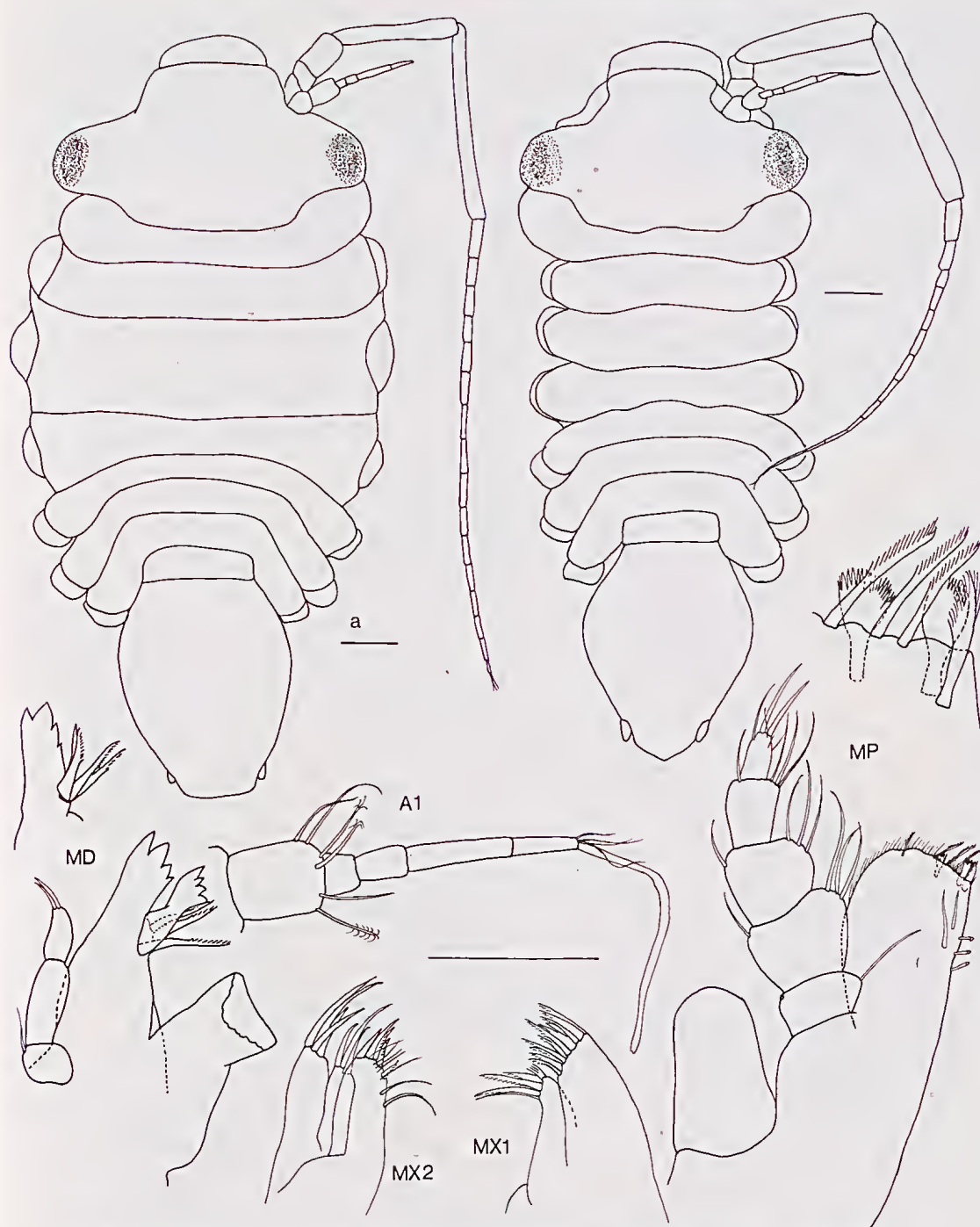


Fig. 7 — *Uromunna brevicornis*. Male, 1.29 mm, NMVJ1057; a, female, 1.32 mm, NMVJ1056.

setose, 2 stronger setae on apex. Pleopod 4 with 2-articled exopod bearing 2 long setae terminally.

Uropod without peduncle; lower ramus with about 8 setae; upper ramus minute and with 1 seta.

Female. Pereon twice as long as wide; pereonites 3

and 4 wider than others, pereonite 1 without developed shoulders. Head a little wider than pereonite 1.

Antenna and mouthparts as in male.

Pereopod 1 similar to that of male but article 5 usually with 5 spines. Pereopod 2 much finer than in



Fig. 8—*Uromunna brevicornis*. Male, 1.29 mm, NMVJ1057.

male; article 5 with 3 evenly-spaced posterior spines; article 6 with 7 evenly-spaced posterior spines. Pereopods 3-7 slightly finer than in male.

Pleopod 2 truncate-rounded, little longer than wide. Pleopods 3-5 as in male.

REMARKS: These Victorian specimens are assigned to the

Western Australian species on the basis of fair resemblance to Thomson's (1946) figures and descriptions; type material can no longer be found. In particular, the dentition of the first pereopod, characteristic narrow form of the male, and form of the pleopods correspond well. Thomson's figures and description of the second pereopod are based on a male, not a female as in-

licated. Further support for the identity of this species comes from the similar estuarine environment in which the species is found. Another estuarine isopod, *Syn-cassidina aestuaria* Baker, also occurs in both eastern and western Australia (Poore 1982). On the other hand *Cruranthura peroni* (Poore), also known from the Gippsland Lakes, differs in subtle ways from *C.*

simplicia Thomson described from the same locality as *U. brevicornis* (Poore in press). One attempt by me in May 1983 to obtain topotypic material was unsuccessful possibly because of unusually high salinity.

Uromunna brevicornis is most similar to *U. nana* (Nordenstam) from the Falkland Islands and *U. schauinslandi* (Sars) from New Zealand. The most

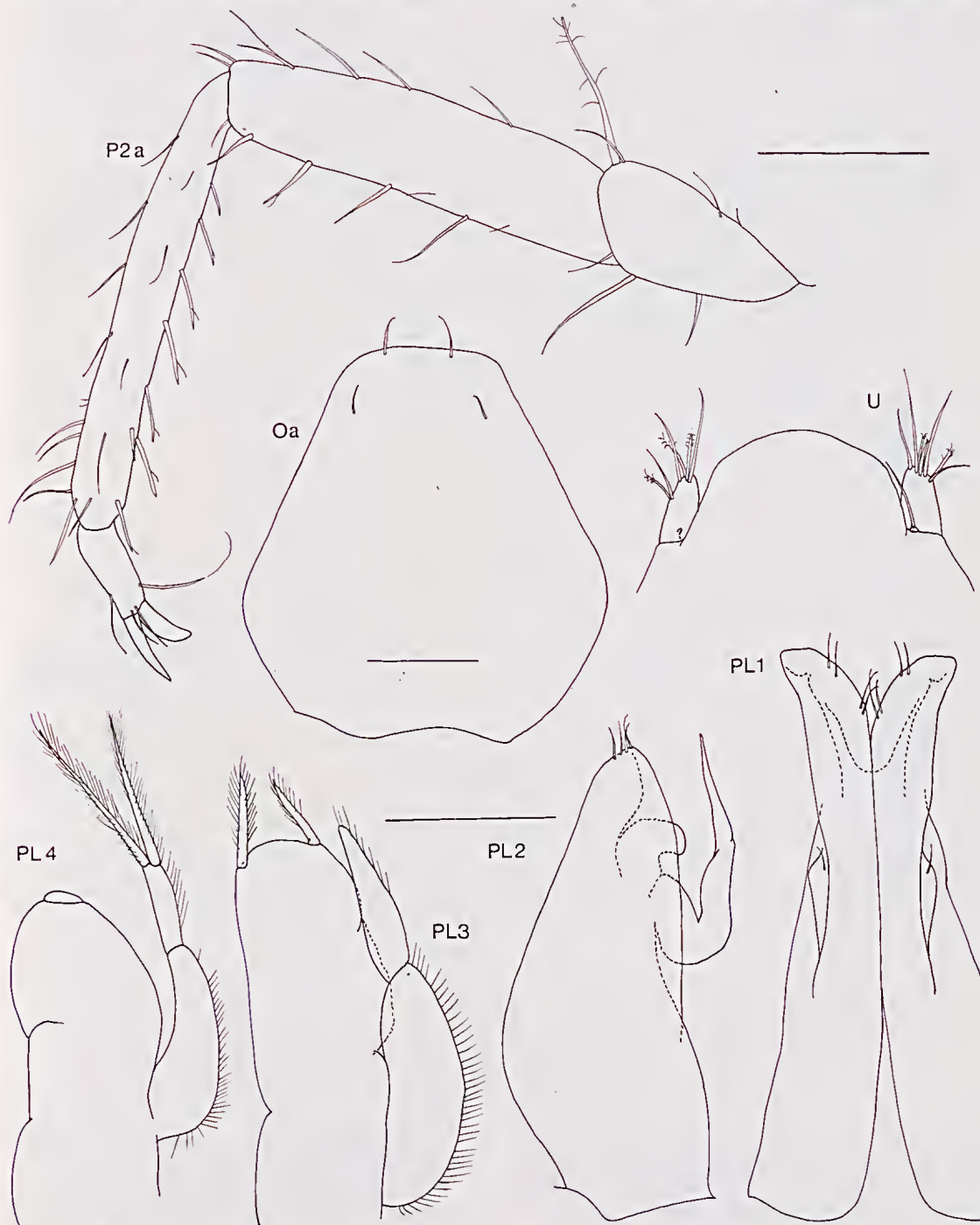


Fig. 9—*Uromunna brevicornis*. Male, 1.29 mm, NMVJ1057; a, female, 1.29 mm, NMVJ1062.

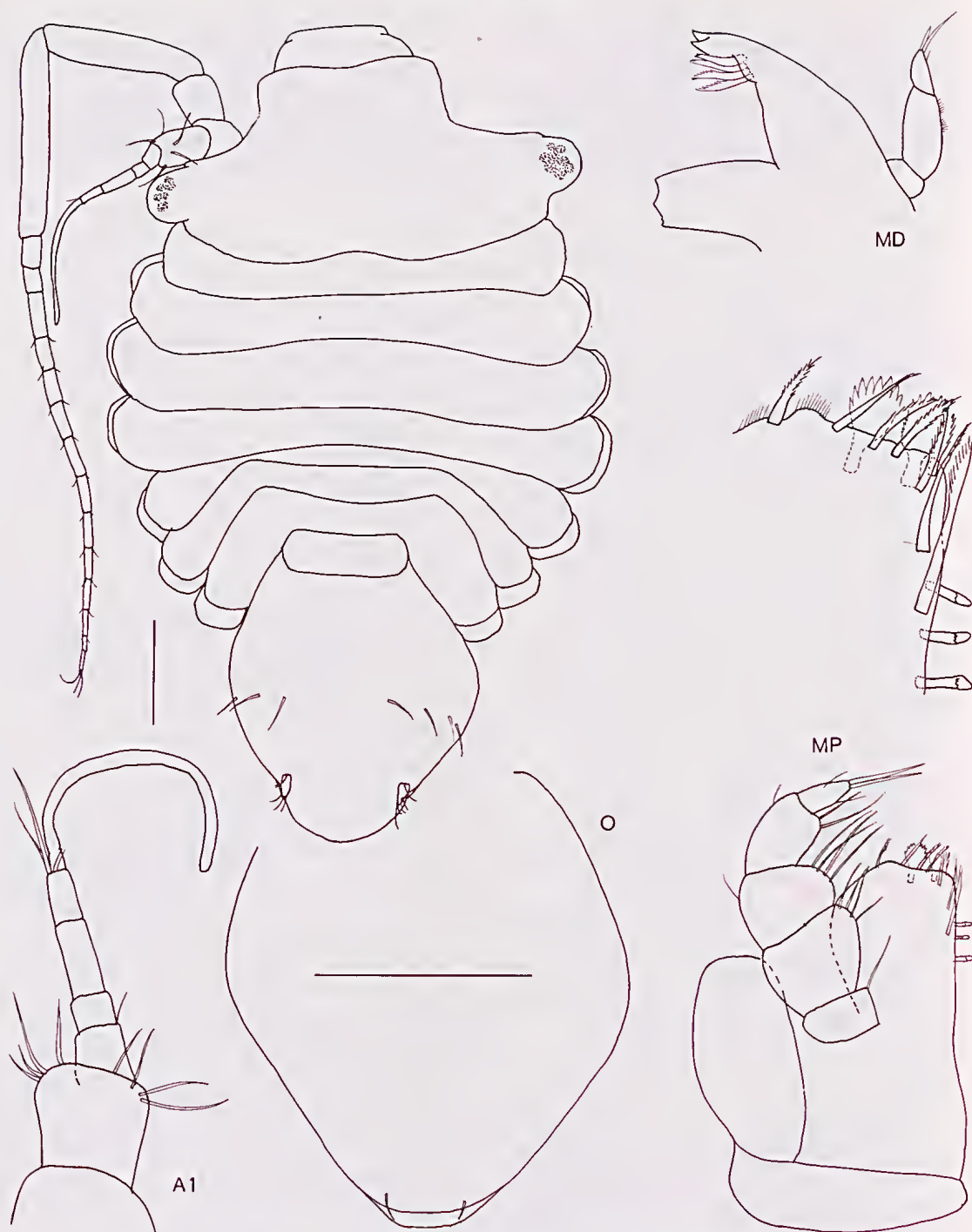


Fig. 10—*Uromunna humei*. Female, 0.74 mm, NMVJ1069.

significant difference is in development of male pereonite 1, not apparent in Menzies (1962) figures of *U. nana* nor in specimens of *U. schauinslandi* (NMVJ3701) dissected by me. *Uromunna schauinslandi* is morphologically very similar, for example in the form of pleopod 1 and pereiopods, but the differences in setation are adequate

to distinguish the species. Both *U. brevicornis* and *U. schauinslandi* are estuarine species.

Uromunna brevicornis shows well the sexual dimorphism of pereiopod 2 which is characteristic of the genus. The species is distinguished from the other species described here by the presence of denticles on the palm of the first pereiopods.

***Uromunna humei* sp. nov.**

Figs 10-12

MATERIAL EXAMINED: *Holotype*: female, 0.74 mm, NMVJ1069. Vic., Apollo Bay (38°45'S., 143°41'E.), from coralline algae in intertidal pools, W. F. Seed, 22 Dec. 1970. *Paratype*: Vic., type locality, NMVJ1070 (1 male, 0.65 mm).

DESCRIPTION: *Female*. Body 1.5 times as long as wide. Pereonites 3-5 wider than others. Head little wider than pereonite 1; anterior margin straight, upper lip projecting anteriorly. Pleon with short free first pleonite; pleotelson globose, about as wide as long, with transverse row of 8 setae. Integument largely without setae, with brown mid-dorsal stripe on pereon.

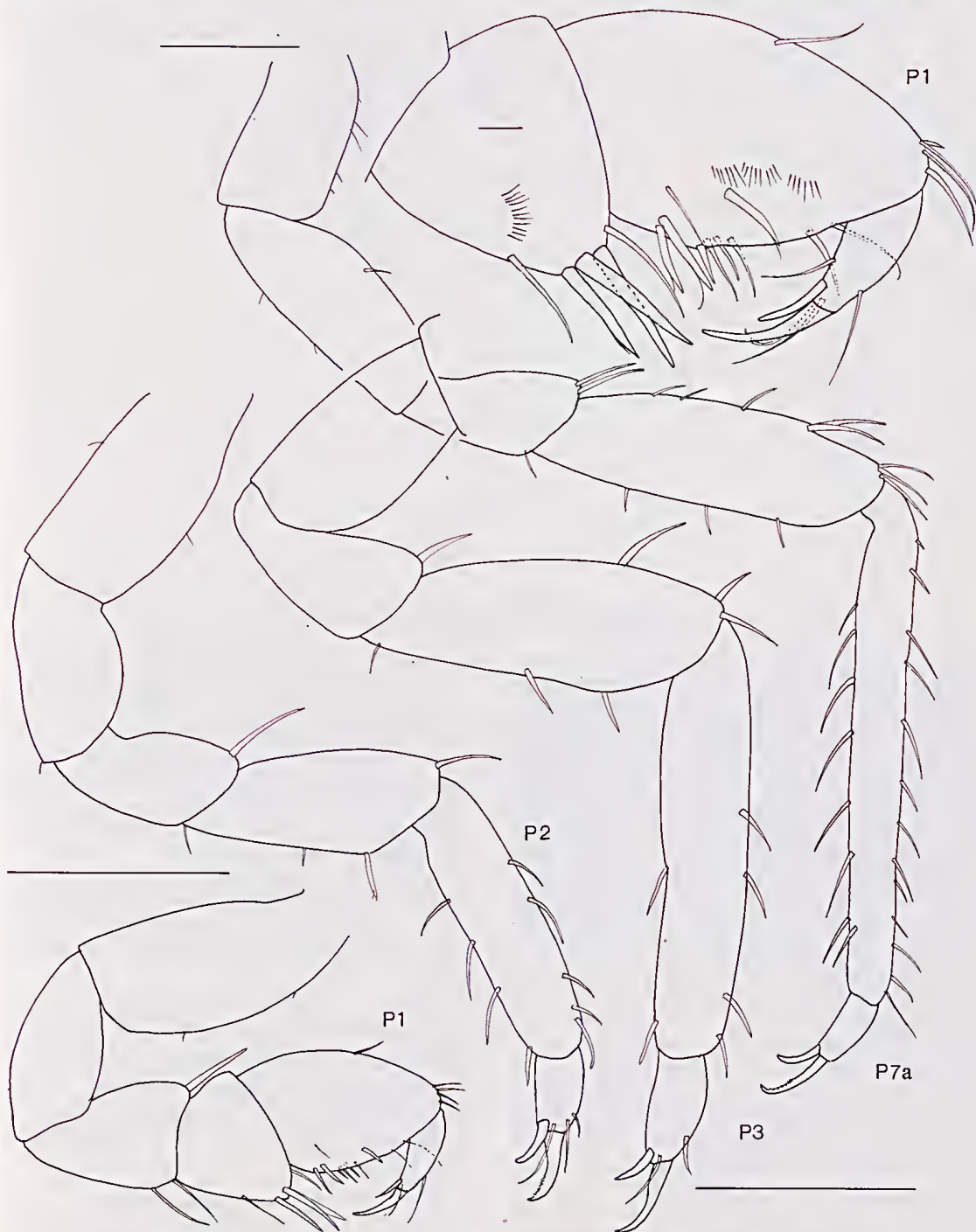


Fig. 11 — *Uromunna humei*. Female, 0.74 mm, NMVJ1069; a, male, 0.65 mm, NMVJ1070.

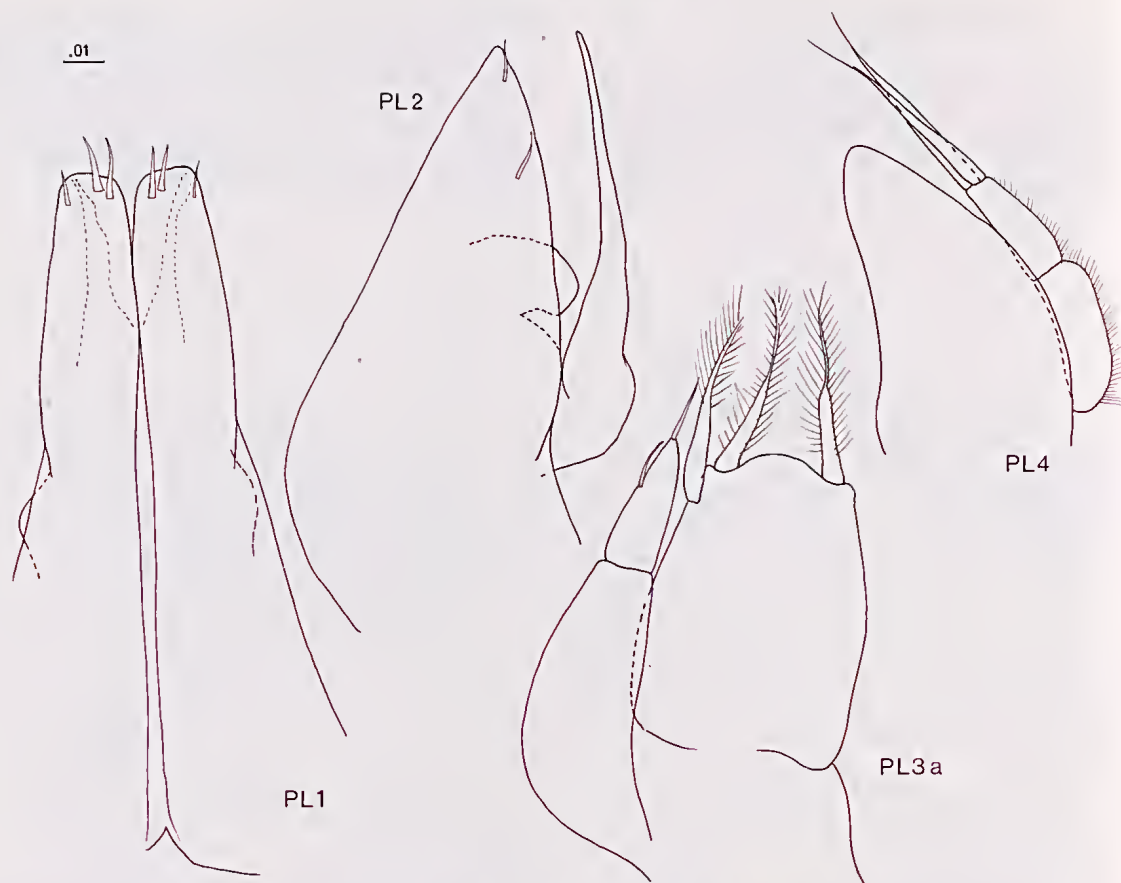


Fig. 12—*Uromunna humei*. Male, 0.65 mm, NMVJ10; female, 0.74 m, NMVJ1069.

Antenna 1 with 2 broad basal articles, 2 short and narrower articles plus flagellum of 2 narrow tapering articles, of which the last one bears 1 aesthetasc. Antenna 1 peduncle of 3 short broad articles and 2 elongate articles; flagellum of 14 articles, as long as rest of peduncle; total length of antenna about as long as body. Mandible with a 3-articled palp, not reaching to end of incisor, the terminal article with 2 setae; incisor, lacinia mobilis and setal row typical of genus; molar tuberculate, without spines. Maxilla 1 inner ramus with 5 spines, outer ramus with 7 spines. Maxillipedal epipod oval, reaching to end of second palp article; endite with 4 distal spines, 3 submarginal fan-shaped setae, 3 setae near mesial margin and 3 retinaculæ; palp of 5 articles, first four with 1, 4, 4 and 2 mesial setae, last article with 2 setae and 2 spines.

Pereopods 1 symmetrical, much smaller than other limbs. Pereopod 1 article 4 with 1 anterodistal spine; article 5 with 3 posterodistal spines; article 6 palm convex with 3 spines on mesial face, and marginal setae; dactyl with unguis about as long as rest of dactyl, plus short supplementary spine. Pereopod 2 article 4 with 1 anterior spine; article 5 with 1 anterior and 2 posterior spines; article 6 with anterior setae and 4 posterior spines; dactyl 3 times as long as wide, with fine unguis as long as rest of dactyl, plus shorter supplementary claw.

Pereopod 7 similar to pereopod 2 but more elongate and with more spines; article 6 is 10 times as long as wide.

Pleopod 2 as long as wide, widest at midpoint, with 2 subapical setae. Pleopod 3 endopod with 3 stout apical setae; exopod narrower than endopod, of 2 articles of which the last is short and bears 2 setae. Pleopod 4 exopod of 2 articles, the last with 2 long apical setae.

Uropod without peduncle; lower ramus with about 6 setae; upper ramus not seen.

Male. Like female except for pleopods. Pleopod 1 evenly tapering to rounded-truncate apices; each apex with 3 subterminal setae. Pleopod 2 apex acute, with 2 setae along mesial edge. Pereopod 2 not present on only male.

ETYMOLOGY: *Munna humei* is named for Hamilton Hume (1797-1873) who, in 1824 with William Hovell, explored from Sydney as far as Port Phillip Bay.

REMARKS: *Uromunna humei* is superficially similar to *U. phillipi* described here. The most obvious differences are in the much longer head and stouter dactyls on pereopods 2-7.

Uromunna phillipi sp. nov.

Figs 13-15

1975 *Munna* sp. Poore *et al.*, pp. 32, 63.

MATERIAL EXAMINED: *Holotype*: female, 1.16 mm, NMVJ1073. Vic., Port Phillip Bay (37°57.7'S., 144°44.7'E.), sand, 5 m (PPBES stn 907), Marine Pollution Studies Group, Ministry for Conservation, 3 Feb. 1972. *Paratypes*: Vic., type locality, NMVJ1074-6 (4 females, 1.0-1.1 mm). *Other material*: Tas., Fancy

Point, on algae, 3 m, G. Edgar, 10 Dec. 1980, NMVJ1580 (11 females), NMVJ1614 (1 male).

DESCRIPTION: *Female*. Pereonites 2 and 3 wider than others. Head about as wide as pereonite 1; anterior margin straight, upper lip distinct and projecting in



Fig. 13—*Uromunna phillipi*. Female, 1.13 mm, NMVJ1075; a, female, 0.98 mm, NMVJ1074.

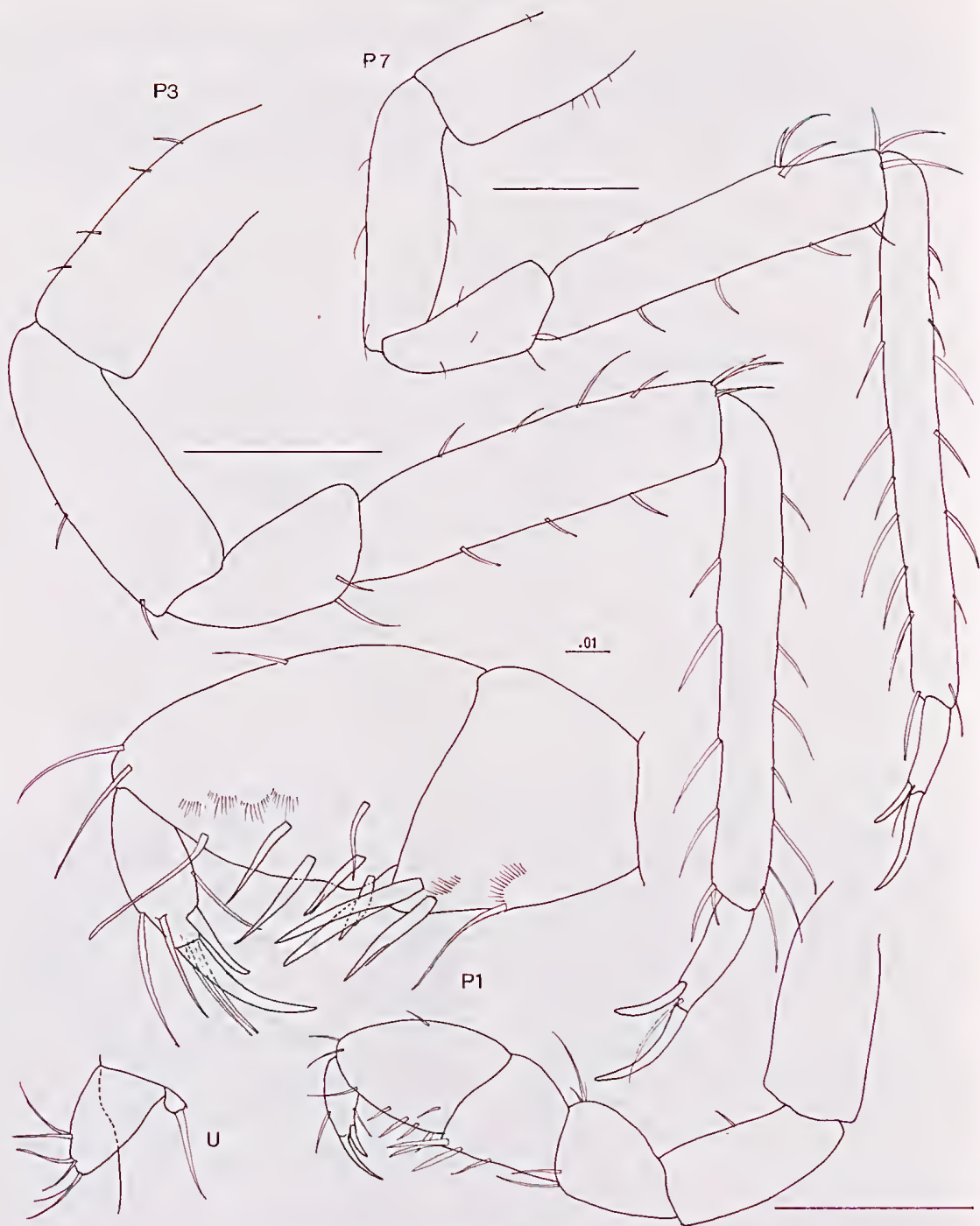


Fig. 14—*Uromunna phillipi*. Female, 1.13 mm, NMVJ1075.

front of head. Pleon with single free first pleonite; pleotelson globose, 1.3 times as long as wide. Integument largely without dorsal setae, except on pleotelson; with diffuse brown colour.

Antenna 1 with 2 broad basal articles, 2 short narrow articles, and 2 longer narrow articles of which the sec-

ond is half the length of the first; aesthetasc on the end of the terminal article. Antenna 2 peduncle of 3 short basal articles and 2 elongate articles; flagellum of 12 articles, a little shorter than peduncle; total antenna about as long as body. Mandible with 3-articled palp not reaching end of incisor, first article with 1 seta, last

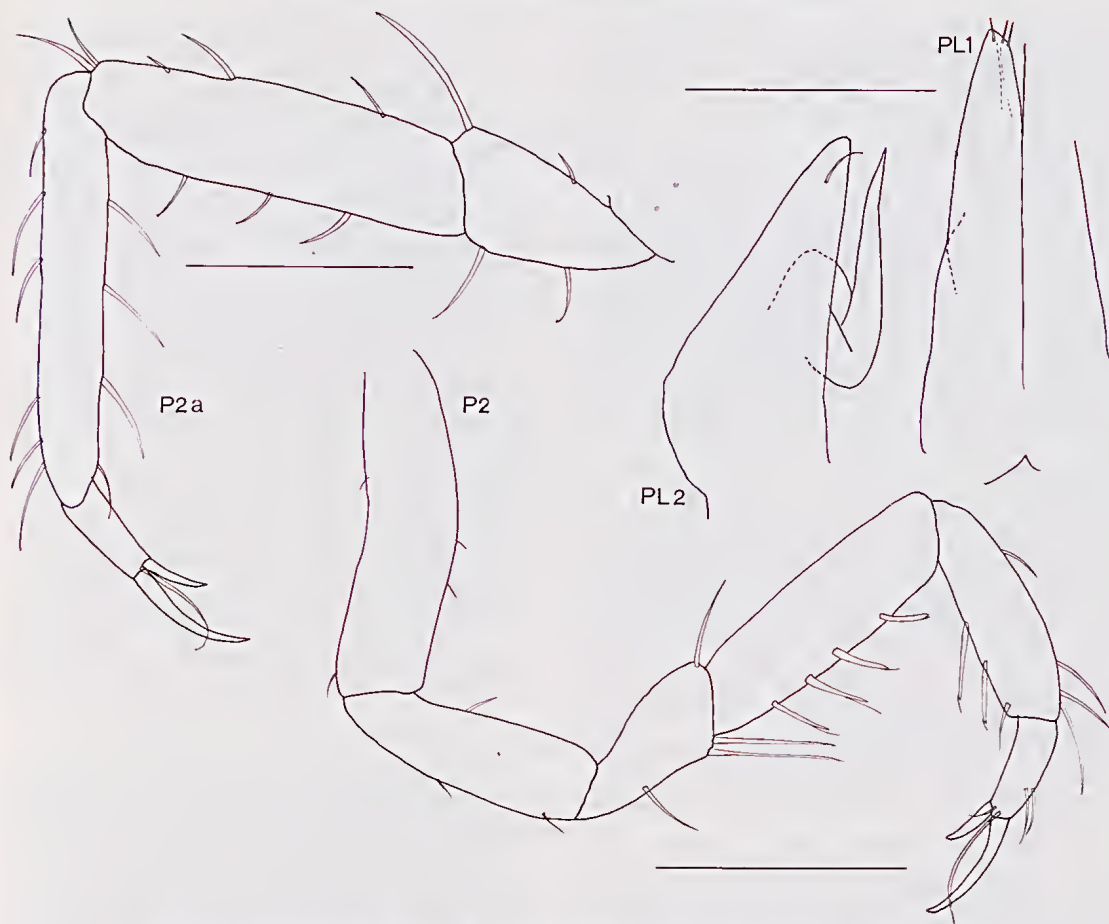


Fig. 15—*Uromunna phillipi*. Male, 0.7 mm, NMVJ1614; a, female, 1.13 mm, NMVJ1075.

article with 2 terminal setae; incisor of 4 cusps; lacinia mobilis on one side only, with 4 teeth; spine row of 3-4 spines; molar process prominent, with tuberculate grinding surface and without setae. Maxilla 1 inner ramus with 4 spines and outer ramus with 11 spines. Maxilla 2 rami with distal simple and complex setae extending mesially along inner ramus. Maxillipedal epipod oval, reaching second article of palp; endite with 4 distal spines, 3 submarginal fan-shaped setae, 3 spines along mesial margin and 3 retinaculae; palp of 5 articles, first four with 1, 3, 4 and 2 setae mesially, last article with 4 setae and 2 spines.

Pereopods 1 symmetrical, much shorter than following legs; article 4 with anterodistal spine; article 5 with 3 posterodistal spines; article 6 with barely-convex palm with 1 proximal spine, 3 spines on mesial face and 1 seta distally; dactyl with spine at base of unguis; unguis half length of dactyl. Pereopods 2-7 increasing in length posteriorly. Pereopod 2 article 4 with long anterodistal spine; article 5 with 4 evenly-spaced spines on posterior margin and 3 on anterior margin; article 6 with 4 spines on posterior margin; dactyl 6 times as long as wide, with very fine unguis as long as rest of dactyl, and shorter

supplementary claw. Pereopod 3 similar, but more elongate than pereopod 2. Pereopod 7 article 4 with 2 anterodistal spines; article 5 with 4 posterior spines and 2 groups of 3 spines anteriorly; article 6 is 10 times as long as wide, with 8 spines anteriorly and 8 posteriorly; dactyl with very fine unguis a little shorter than rest of dactyl, and very fine supplementary claw.

Pleopod 2 subtriangular, with 2 subapical setae. Pleopod 3 endopod with 3 plumose setae; exopod much narrower, of 2 articles both marginally setose, 1 strong seta on apex. Pleopod 4 endopod subacute; exopod narrow, tapering, with a long terminal seta.

Uropod without a peduncle; lower ramus with 7 setae; upper ramus minute, with 1 seta.

Male. Differing from female only in pereopod 2, pleopods 1 and 2. Pereopod 2 distal articles broader than in female, article 5 with 4 spines on posterior margin, article 6 with 3 spines. Pleopod 1 tapering to simple, obliquely truncate apex, each half with 3 setae. Pleopod 2 apex rounded-acute, with 1 subterminal seta. Pleopods 3-5 as in female.

ETYMOLOGY: *Uromunna phillipi* is named for Arthur Phillip (1738-1814), first Governor of New South Wales.

REMARKS: *Uromunna phillipi* is distinguished from *U. humei* by its shorter head and finer dactyls on pereopods 2-7. The male figured is from Tasmania.

ACKNOWLEDGEMENTS

I am indebted to W. Seed, Royal Melbourne Institute of Technology, who provided some of the material on which this study is based. I thank Helen Lew Ton who prepared some of the figures. J. Lowry and B. Kensley read an earlier draft of this paper and provided much useful criticism for which I am most grateful. R. Lincoln (British Museum (Natural History)), B. Kensley (Smithsonian Institution), B. Louw (South African Museum) and M. Christiansen (Zoologisk Museum, Oslo) kindly lent type-specimens for examination.

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APPENDIX

SPECIES OF MUNNA AND UROMUNNA

The list includes species assigned to *Zoromunna* (as *Munna*) but not species of *Astrurus* or *Echinomunna*. As well as those species listed several others have been described in the genus *Munna*. *Munna brandti* Zirwas 1916, *M. dentata* Vanhöffen 1914, *M. studeri* Hilgendorf 1893, are not sufficiently well described to be placed with confidence. Kensley (1975, 1976) and Wilson (1980) each listed two additional species but did not describe them. Also in this group is *M. concavifrons* (Barnard 1920), originally described as a species of *Paramunna*. Descriptions of *Munna* sp. A. Monod 1933, and *Munna* sp. Stephensen 1947, could not be obtained and they too remain unplaced. Two other species have already been removed to other genera: *Munna caeca* Richardson 1905, to *Haplomunna* Richardson (Wolff 1962) and *Munna* sp. B Monod 1933, to *Antias milleri* Menzies & Glynn 1968 (= *Santia milleri*). *Munna argentiniae* Menzies 1962 differs from all other species in being without eyes, eyestalks, and mandibular palp. It is superficially not similar to *M. acanthifera*, another blind abyssal species, and its generic affiliation remains in doubt. Another problematical species is *Munna coxalis* Kussakin 1972. The flattened body, coxal projections, extraordinarily long uropods (with two articles?) suggest it too belongs in another genus.

An asterisk (*) against a species indicates that I have seen specimens of this taxon.

Species of *Munna* Krøyer

M. acanthifera Hansen 1916—Arctic; *M. aculeata* Sivertsen & Holthuis 1980—Tristan da Cunha; *M. affinis* Nordenstam 1933—South Georgia; *M. antarctica* (Pfeffer 1887)*—Antarctica; *M. armoricana* Carton 1962—France, Channel coast; *M. arnholdi* Gurjanova 1933—Kurile Islands; *M. avatshensis* Gurjanova 1936—NW Pacific; *M. bituberculata* Nordenstam 1933—South Georgia; *M. boeckii* Krøyer 1839*—NW Atlantic; *M. chilensis* Menzies 1962—S Chile; *M. chromatoccephala* Menzies 1952—California; *M. chromatoccephala inornata* Kussakin 1962—E USSR; *M. chromatoccephala orientalis* Kussakin 1974—NW Pacific; *M. coeca* Gurjanova 1930—Spitsbergen; *M. crinata* Kussakin 1972—Kurile Islands; *M. cryophila* Vanhöffen 1914—Antarctica; *M. fernaldi* George & Strömberg 1968—Washington; *M. globicauda* Vanhöffen 1914—Antarctica; *M. greonlandica* Hansen 1916—Greenland; *M. halei* Menzies 1952—California; *M. hanseni* Stappers 1907—Iceland; *M. hentyi* sp. nov.—SE Australia; *M. hirsuta*

Kussakin 1962—Kurile Islands; *M. hovelli* sp. nov.—SE Australia; *M. humei* sp. nov.—SE Australia; *M. instructa* Cleret 1971—Marion Island; *M. kroyeri* Goodsir 1942*—NE Atlantic; *M. kurilensis* Kussakin 1974—NW Pacific; *M. limicola* Sars 1868—N Europe; *M. lobata* Kussakin 1962—E USSR; *M. lukini* Kussakin & Mezhev 1979—NW Pacific; *M. lundae* Menzies 1962—S Chile; *M. macquariensis* Hale 1937*—Macquarie Island; *M. maculata* Beddard 1886—Kerguelen and Falkland Islands; *M. magnifica* Schultz 1964—California; *M. minuta* Hansen 1916—N Atlantic; *M. modesta* Kussakin 1962—E USSR; *M. nasuta* Kussakin & Mezhev 1979—NW Pacific; *M. neglecta* Monod 1931—S Atlantic; *M. neozelanica* Chilton 1892—New Zealand; *M. neozelanica* Barnard 1965—Tristan de Cunha, Gough Island; *M. ornata* Kussakin 1962—E USSR; *M. pallida* Beddard 1886—Kerguelen and Falkland Islands; *M. palmata* Liljeborg 1851—Norway; *M. parvituberculata* Kussakin 1962—E USSR; *M. pellucida* Gurjanova 1930—Barents Sea; *M. psychrophila* Vanhöffen 1914—Antarctica; *M. roemeri* Gurjanova 1930—?; *M. serrata* Kussakin 1962—E USSR; *M. setosa* Kussakin 1962—E USSR, Kurile Islands; *M. spinifera* Robinson & Menzies 1961—Gulf of Aden; *M. spinifrons* Menzies & Barnard 1959—California; *M. spitzbergensis* Gurjanova 1930—Spitsbergen; *M. stephenseni* Gurjanova 1933—Bering Sea; *M. stephenseni* Menzies 1962—California; *M. subneglecta* Gurjanova 1936—Sea of Japan; *M. tenuipes* Kussakin 1962—E USSR; *M. truncata* Richardson 1908—NW Atlantic; *M. uncinata* Kussakin & Mezhev 1979—NW Pacific; *M. urupica* Kussakin 1972—Kurile Islands; *M. varians* Sivertsen & Holthuis 1980—Tristan da Cunha; *M. vittata* Kussakin & Mezhev 1979—NW Pacific; *M. wolffi* Fresi & Mazzella 1974—Italy; *Munna* sp. Monod 1931—South Georgia.

Species of *Uromunna* Menzies

U. acarina (Miller 1941)—Hawaii; *U. brevicornis* (Thomson 1946)*—S Australia; *U. caribea* (Carvacho 1977)—Caribbean; *U. hayesi* (Robertson 1978)—Texas; *U. nana* (Nordenstam 1933)—Tristan da Cunha, Falkland, St Paul and Amsterdam Islands; *U. nana* Forma 'a' (Menzies 1962)—S Chile; *U. petiti* (Amar 1948)—Mediterranean; *U. phillipi* sp. nov.—SE Australia; *U. powelli* (Kensley 1980)*—Nigeria; *U. reynoldsi* (Frankenberg & Menzies 1966)—Gulf of Mexico, Panama Canal; *U. santaluciaae* (Gascón & Mañé-Garzón 1974)—Uruguay; *U. schauinslandi* (Sars 1905)*—New Zealand; *U. schauinslandi* (Menzies 1962)—S Chile; *U. sheltoni* (Kensley 1977)*—South Africa; *U. ubiquita* (Menzies 1952)*—Washington, California.

STUDIES ON WESTERN AUSTRALIAN PERMIAN BRACHIOPODS

4. PRODUCTELLIDAE SCHUCHERT & LE VENE 1929 AND OVERTONIIDAE MUIR-WOOD & COOPER 1960

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ABSTRACT: Productellidae and Overtoniidae (Productida, Brachiopoda) from the Early Permian sequences of the Carnarvon Basin, Western Australia are described. The following species are revised or described: *Stictozoster senticosa* (Hosking), *Comuquia australis* sp. nov., *?Lethamia obscurus* sp. nov., *Dyschrestia micracantha* (Hosking), *Dyschrestia colemani* sp. nov. and *Dyschrestia* sp.

This paper continues the series of studies on Western Australian Permian brachiopods (Archbold 1983). Representatives of the Productellidae and the Overtoniidae are restricted to the early Permian sequence of the Carnarvon Basin. None of the species are common. The stratigraphy of the Carnarvon Basin is documented in references referred to in Archbold (1981, p. 109). The basis for age assignment of species is also outlined in Archbold (1981). Terminology is standard as in previous studies.

COLLECTIONS

All figured and measured specimens are housed in the following institutions as indicated by the prefix to the registered numbers. CPC—Commonwealth Palaeontological Collections of the Bureau of Mineral Resources, Geology and Geophysics, Canberra, A.C.T. GSWA—Geological Survey of Western Australia, Perth, Western Australia. MUGD—Department of Geology, University of Melbourne, Parkville, Victoria.

SYSTEMATIC PALAEONTOLOGY

Order PRODUCTIDA Sarycheva & Sokolskaya 1959
Superfamily PRODUCTELLACEA Schuchert & Le Vene 1929

?Family PRODUCTELLIDAE Schuchert & Le Vene 1929

Genus **STICTOZOSTER** Grant 1976

TYPE SPECIES: *Stictozoster leptus* Grant 1976.

DIAGNOSIS: The diagnosis provided by Grant (1976, p. 96) is accepted.

DISCUSSION: Grant (1976) discussed the combination of features of this peculiar genus, noting that *Stictozoster* does not fit readily into any established family, however, the present author follows Grant and retains the genus provisionally within the Productellidae, 'extending the range of that family on somewhat doubtful grounds' (Grant 1976, p. 96).

Grant (1976) referred no other species to this genus although he did indicate that *Pustula senticosa* Hosking 1933 belonged to *Stictozoster*, an indication substantiated herein. Several other species, although known only from ventral valves, appear distinctive enough to assign to *Stictozoster*, as summarised by Archbold,

(1982b, p. 9) and, in part, independently by Waterhouse (1981, p. 74). Waterhouse (1981) however, disputed the generic position of *S. senticosa* and suggested that the species belonged in *Lethamia*, a genus that has subsequently been fully described and figured (Waterhouse 1982a). *Lethamia ligurritus* (see Waterhouse 1982a, pl. 8, figs c-i; pl. 9, figs a-j) is of comparable size to *Stictozoster senticosa* but the dorsal septum of *S. senticosa* is delicate, thin and not raised anteriorly as in *Lethamia*. The large size of the only available dorsal valve of *S. senticosa* (width 30.6 mm) indicates that the specimen is not a juvenile. The dorsal septum of *S. senticosa* together with the concentric bands of minute pustules strongly resembles those of *Stictozoster leptus* (Grant, 1976, pl. 17, figs 18, 19). The main difficulty in assigning '*Pustula*' *senticosa* to *Stictozoster* is the ornament of external coarse spines (much coarser than those of *S. leptus* and species of *Lethamia*), but the dorsal interior features are taken to be more diagnostic. The cardinal process of *Lethamia* appears to be similar to that of *Stictozoster*.

Stictozoster senticosa (Hosking 1933) Fig. 1A-H

- 1933 *Pustula senticosa* Hosking, p. 47, pl. 3, figs 2-3.
1937 *Pustula senticosa* Hosking; Raggatt and Fletcher. *Rec. Aust. Mus.*, 20: 176.
1943 *Krotovia senticosa* (Hosking); Prendergast, p. 30.
1957 *Krotovia senticosa* (Hosking); Coleman, p. 63, pl. 7, figs 11-15.

LECTOTYPE: GSWA1/4970a1; Hosking, 1933, pl. 3, figs 2a, b. Chosen by Coleman (1957, p. 63).

MATERIAL, AGE AND LOCALITY: Hosking's (1933) syntypic series of 3 conjoined shells, all crushed, 1 with much of the dorsal interior exposed, GSWA 1/4970a1-1/4970a3, all from creek 0.75 km west of Callytharra Springs, Wooramel River; Callytharra Formation; Sterlitamakian (Late Sakmarian).

MEASUREMENTS (in mm): Lectotype*, e = estimate

Specimen number	Maximum width	Hinge width	Ventral height	Dorsal height
GSWA1/4970a1*	23.5	16.7	17.1	15.5
GSWA1/4970a2	30.6	22.0	23.2	20.8
GSWA1/4970a3	28 e.	20 e	20.6+	18.0+

DIAGNOSIS: Large *Stictozoster* with coarse spines widely spaced. Dorsal interior characteristic of genus.

DESCRIPTION: Outline transversely subelliptical; shell concavo-convex, visceral cavity thin, non-geniculate; hinge width about two-thirds of maximum width, hinge ends rounded; valves thin, no thickening at hinge; maximum width at midlength of shell; both valves covered with spines, those of dorsal valve being finer; ventral spines undifferentiated, arranged in concentric rows of fine concentric growth lines, concentric rows spaced at 0.5 to 0.75 mm anteriorly and spines spaced at 1 to 1.5 mm; anteriorly, posterior spacing of rows and spines both 0.5 to 0.75 mm; most spines erect; dorsal spines spaced more irregularly along concentric rows; dorsal valve with shallow dimples; concentric ornament of growth lines fine on ventral valve, more pronounced on dorsal valve; ventral beak fine, curved over hinge line.

Ventral interior unknown. Dorsal interior with small productellacean cardinal process, bilobed with lobes incised, shaft with alveolus; median septum low, thin, less than one-third valve length; muscle pad low, rounded; brachial ridges indistinct; endospines short, erect, arranged in concentric rows.

DISCUSSION: *Stictozoster senticosa* is atypical of the genus because of its larger size and relatively coarser and more widely spaced spines.

Coleman (1957) considered that the ventral spines are arranged quincuncially but this is because the spines are arranged in concentric rows, each being offset from the preceding row and as spines are coarser and more widely spaced than those of other species of the genus a quincuncial arrangement becomes evident. No other known species of *Stictozoster* possesses spines as coarse as those of *S. senticosa*; both *S. nielsenii* (Dunbar) and *S. licharewii* (Frebold) possess ventral spines similar to those of *S. leptus* with respect to their size and arrangement (see Archbold 1982b) and the *Stictozoster* sp. cf. *S. leptus* from Irian Jaya is even closer to the type species (Archbold *et al.* 1982).

Family OVERTONIIDAE Muir-Wood & Cooper 1960

Subfamily OVERTONIINAE Muir-Wood & Cooper 1960

DIAGNOSIS: The diagnosis provided by Muir-Wood & Cooper (1960, p. 183) is accepted.

DISCUSSION: Waterhouse (in Bamber & Waterhouse

1971) recognized the Tubersulculinae within the Overtoniidae, differentiating the subfamilial groupings on the strength of the concentric lamellae and the degree to which the ventral spines are concentrically arranged. However, several genera (e.g. *Dyschrestia*) are now known to be intermediate in these features and the subfamily groupings are not employed herein.

Genus COMUQUIA Grant 1976

TYPE SPECIES: *Comuquia modesta* Grant 1976.

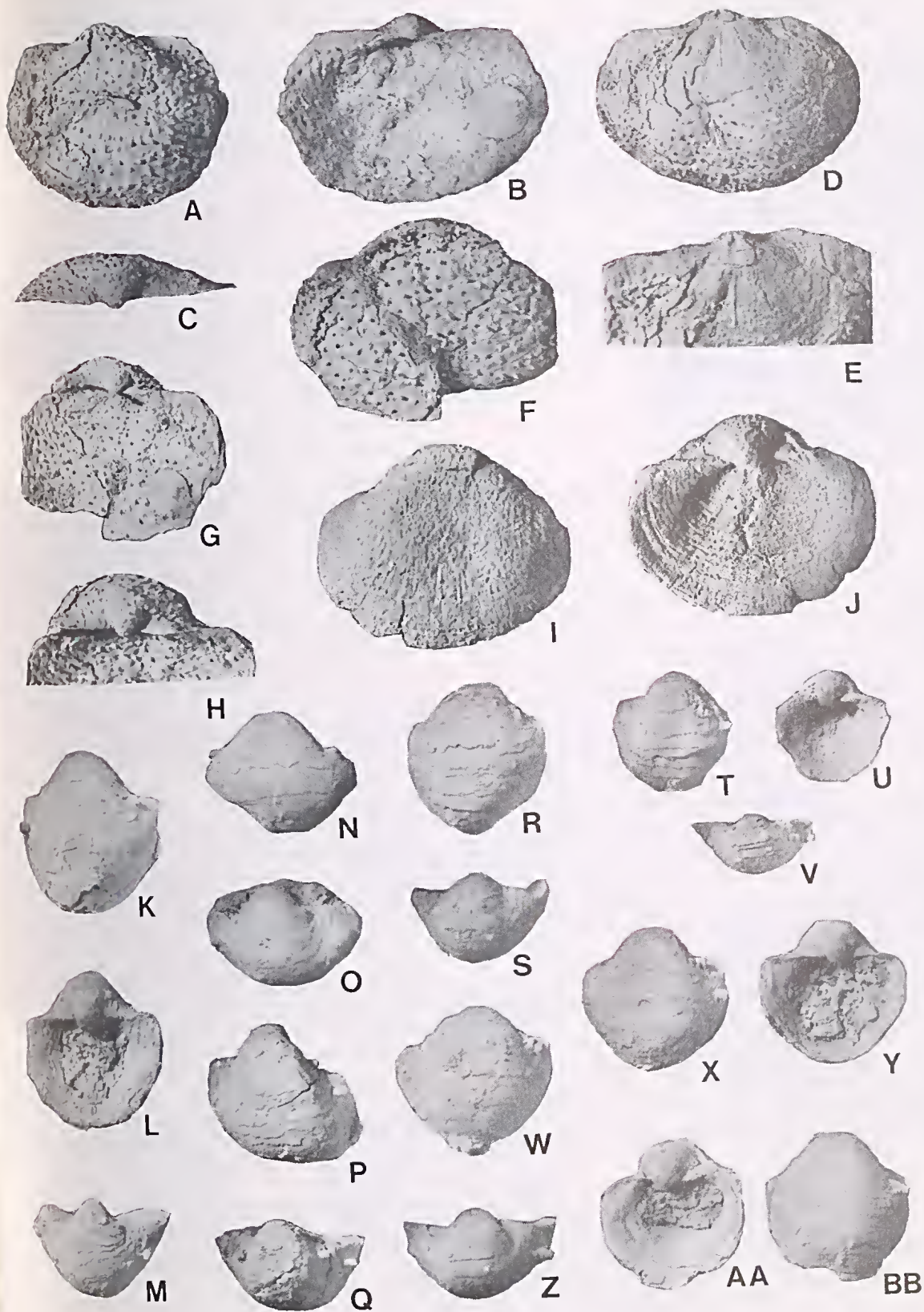
DIAGNOSIS: Small, elongate ovate; widest near midlength; growth lamellae strong, irregular; ventral spines variable in number, projecting from growth lamellae; dorsal spines few to absent; dorsal valve deeply concave; ventral valve strongly convex. Cardinal process bilobed with stout shaft; median septum thin, low; brachial ridges absent. (Revised from Grant 1976).

DISCUSSION: *Comuquia modesta* was well described by Grant (1976), however, the diagnosis of the genus requires broadening in order to include the new species *Comuquia australis* which is similar to the type species in its shell outline, concavo-convexity, growth lamellae and umbonal characteristics, but differs in possessing far fewer spines and in having a non spinose dorsal valve.

Rhythisia Cooper & Grant (1975, p. 967, pl. 311, figs 15-59) from the early Kungurian of Texas, is related to *Comuquia* yet differs in details of ventral spine pattern and in possessing distinct concentric wrinkles. *Comuquia* recalls *Scoloconcha* Gordon (1966) in details of size, convexity and ventral spinosity, but *Scoloconcha* possesses strongly developed marginal ridges and a trifid cardinal process.

Grant (1976, p. 98) considered *Comuquia* to provide an additional generic category for Permian Overtoniidae that would find wide applicability although he did not compare *C. modesta* with any other species. The group of '*Productus*' *curvirostris* Schellwein (1892, p. 26, pl. 3, figs 12-14) being both widely distributed in space and time, belongs in *Comuquia*. Originally described from possible Asselian strata of the Carnic Alps it is now known from Italy, U.S.S.R., Tien Shan, Karakorum and Thailand.

Fig. 1-A-H, *Stictozoster senticosa* (Hosking) from Callytharra Formation, Carnarvon Basin. A-C, GSWAF1/4970a1, lectotype, crushed shell in ventral, dorsal and posterior views, $\times 1.8$. D-E, GSWAF1/4970a2, crushed shell most of ventral valve missing in ventral view, $\times 1.3$ and enlargement of cardinal region, $\times 2$. F-H, GSWAF1/4970a3, crushed shell in ventral, dorsal and posterior views, $\times 1.5$, $\times 1.4$ and $\times 1.8$ respectively. I-J, ?*Lethamia obscurus* sp. nov. from Callytharra Formation, Carnarvon Basin. I-J, CPC1952, holotype, crushed shell in ventral and dorsal views, $\times 2.2$. K-Z, AA-BB, *Comuquia australis* sp. nov. from Callytharra Formation, Carnarvon Basin. K-M, GSWAF11050, holotype, shell in ventral, dorsal and posterior views, $\times 3.5$. N-O, GSWAF11191, crushed shell in ventral and posterior views, $\times 3.3$. P-Q, CPC19930A, ventral valve in ventral and posterior views, $\times 3.5$. R-S, GSWAF11190, ventral valve in ventral and posterior views, $\times 3.2$. T-V, CPC19930B, ventral valve in ventral, dorsal and posterior views, $\times 3.5$. W, GSWAF11189, ventral valve in ventral view, $\times 3.2$. X-Y, GSWAF11188, ventral valve in ventral and dorsal view, $\times 3.2$. Z, AA-BB, GSWAF11187, shell in posterior, dorsal and ventral views, $\times 3.2$.



***Comuquia australis* sp. nov.**

Fig. 1 K-Z, AA-BB

HOLOTYPE: GSWAF11050, a complete conjoined shell from the type section of the Callytharra Formation.

MATERIAL, AGE AND LOCALITY: GSWAF11050, 11187-11191, 3 conjoined shells and 3 ventral valves from the Callytharra Formation type section at Callytharra Springs. CPC19930A-19930B, 2 ventral valves, same locality, 27-32 m above base of formation; Sterlitamakian (Late Sakmarian).

MEASUREMENTS (in mm): * = holotype

Specimen number	Hinge width	Maximum width	Ventral height	Dorsal height	Thickness
GSWAF11050*	7.4	7.8	7.5	5.5	4.7
GSWAF11187	6.5	6.6	7.4	5.6	4.0
GSWAF11188	6.2	6.3	6.4	5.0	3.8
GSWAF11189	6.9	7.1	7.0	—	4.1
GSWAF11190	5.6	6.1	7.2	—	4.1
GSWAF11191	6.0	—	—	—	—
CPC19930A	5.3	6.9	5.9	—	—
CPC19930B	4.1	5.2	5.4	—	—

DIAGNOSIS: Small *Comuquia* species with distinct lamellae, sparsely spinose ventral valve.

DESCRIPTION: Subovate outline; profile an even spiral; beak prominent, strongly curved; shell widest near midlength; hinge width almost as great as maximum width; dorsal valve deeply concave, outline semicircular; growth lines visible over shell, stronger lamellose growth lines present at irregular intervals on ventral valve; ventral valve sparsely spinose, pair of spines flanking beak; row of up to three lateral spines, widely spaced; ventral spines rare, occasionally up to two on an individual growth lamella towards posterior of valve; dorsal spines apparently absent. Interior of shell unknown.

DISCUSSION: The characteristic outline and profile of this species indicate *Comuquia*; nevertheless *C. australis* is far less spinose than *C. modesta*. Bolkhovitinova and Markov's (1926) report of *Productus curvirostris* from the Sterlitamakian of the Perm region indicates a species particularly close to *C. australis* with respect to details of the beak, shell outline, size and growth lamellae. The Perm species is however more spinose than the Western Australian species although not as spinose as *C. modesta*. The group of *Productus capuloides* Stepanov (1937) possesses few spines on the ventral valve (Tschernyschew 1902, p. 271, pl. 30, figs 1, 2; pl. 53, figs 5, 6) and hence is similar to *C. australis* except for the incipient costae on the anterior of the ventral valve.

C. himalayaensis Jing & Sun (1981, p. 133, pl. 4, figs 17-26) from the early Artinskian Lasaila Limestone of

the southern Himalaya, Tibet has few ventral spines but has a less curved ventral valve than *C. australis*.

Genus LETHAMIA Waterhouse 1973

TYPE SPECIES: *Lethamia ligurritus* Waterhouse 1973.

DIAGNOSIS: The diagnosis provided by Waterhouse (1973, 1982a) is accepted.

?*Lethamia obscurus* sp. nov.

Fig. 1 I-J

1957 *Krotovia* sp. ind. A. Coleman, p. 67, pl. 9, figs 22, 23.

HOLOTYPE: CPC1952, a crushed conjoined shell from the Callytharra Formation, Pell's Range, 24 km north-east of Towrana Homestead; 36 m (i.e. 118 feet) above base of Callytharra Formation (not '180 ft above the Callytharra Formation', as in Waterhouse 1981).

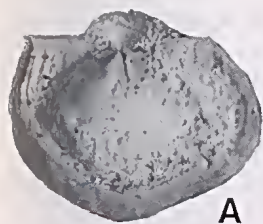
MEASUREMENTS: Maximum width 18.5 mm; hinge width 13 mm; height of dorsal valve 13 mm estimate.

DESCRIPTION: Shell with transversely oval outline; non-geniculate; ventral umbo small, curving over hinge; greatest width anterior of hinge at about shell mid length; convexo-concavity of shell moderate, visceral cavity thin. Ventral valve covered in spines—very fine of uniform size; spines arranged subquincuncially over most of valve, on average 0.75 mm apart and 0.25 mm wide at their base; on anterior of valve spines in concentric rows; rows widely spaced, 1.5-2.0 mm apart. Fine concentric lirae on ventral valve. Dorsal exterior with fine spines and concentric lirae; spines of similar size and arrangement to those of ventral valve. No dorsal dimples. Shell interior unknown.

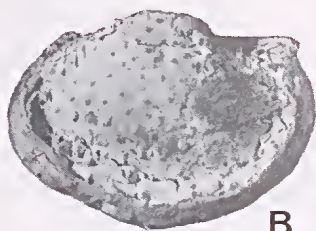
DISCUSSION: Coleman (1957) recognised that this shell represented a distinctive species from Western Australia. Despite additional extensive collections from the Callytharra Formation having been made by Dr G. A. Thomas, University of Melbourne and geologists of the Geological Survey of Western Australia no comparable specimens have been collected. Rather than leave the specimen in open nomenclature it appears advisable to formally name it to highlight its distinctive external morphology. The shell gives no indication of being a sport (e.g. aberrant growth patterns or outline) and is readily distinguishable from all other species.

?*Lethamia obscurus* is closest to *Lethamia* in that it lacks dimples on the dorsal exterior, lacks distinct concentric lamellae and has fine dorsal spines but generic certainty cannot be verified without details of the dorsal interior. Waterhouse (1981, p. 74) and Grant (1976) sug-

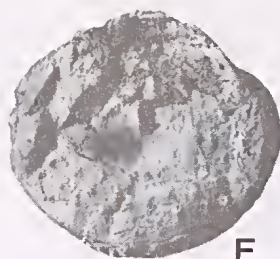
Fig. 2-A-Q, *Dyschrestia micracantha* (Hosking) from Callytharra Formation, Carnarvon Basin. A-B, GSWAF1/4970b2, crushed shell in dorsal and ventral views, $\times 2.2$. C-D, GSWAF1/4970b1, lectotype, crushed shell in dorsal and ventral views, $\times 2.2$. E-F, MUGDF6002, incomplete shell in ventral and dorsal views, $\times 1.8$ and $\times 2$ respectively. G-I, MUGDF6004, crushed shell in dorsal, ventral and posterior views, $\times 2$. J-L, MUGDF6001, crushed shell in ventral, dorsal and anterior views, $\times 1.8$, $\times 2$ and $\times 1.8$ respectively. M-O, CPC1954, dorsal valve in dorsal, ventral and posterior views, $\times 1.6$, $\times 1.8$ and $\times 2.2$ respectively. P-Q, MUGDF6003, crushed shell in dorsal and ventral view, $\times 2$.



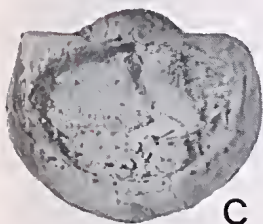
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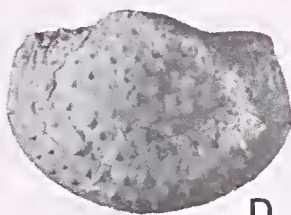
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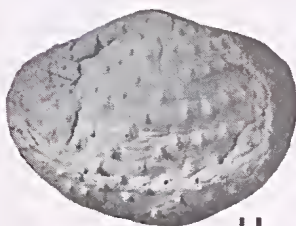
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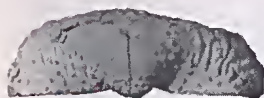
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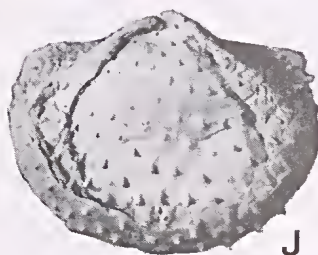
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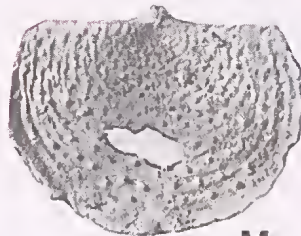
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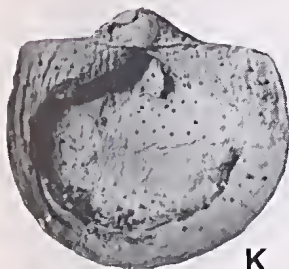
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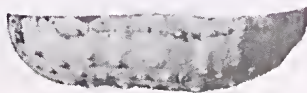
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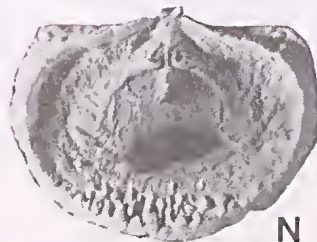
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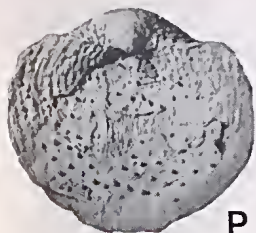
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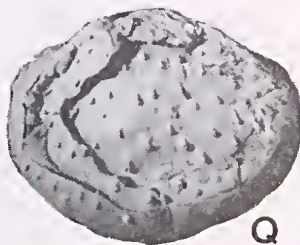
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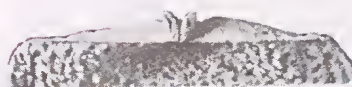
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O

gested that the specimen may belong to *Stictozoster* but that genus possesses distinct dimples and a stronger development of concentric lamellae on the dorsal exterior, also, when the spines are fine on *Stictozoster*, they are dense with the concentric rows being close together. The generic diagnosis of *Stictozoster* has already been enlarged to incorporate *S. senticosa*.

Genus *DYSCHRESTIA* Grant 1976

TYPE SPECIES: *Dyschrestia spodia* Grant 1976.

DIAGNOSIS: The diagnosis provided by Grant (1976) is accepted with the exception that the dorsal interior may possess a distinct marginal ridge, a distinct median septum with a raised anterior termination and raised adductor muscle scars.

DISCUSSION: Grant (1976) compared *Dyschrestia* with several other genera including *Grandaurispina* Muir-Wood & Cooper 1960 and *Holotricharina* Cooper & Grant 1975 of the Linoproductidae which are externally somewhat similar to *Dyschrestia*. Grant noted that *Krotovia* Fredericks 1928 was nearest to *Dyschrestia* in general outline and profile and may well have been a progenitor. *Krotovia* was distinguished from *Dyschrestia* by the more even distribution of spines not tending to be concentrically banded by the presence of growth lamellae, the larger number of dorsal spines and greater development of radial rather than concentric wrinkling due to some species of *Krotovia* having costae bearing spines. The reassessment of *Krotovia* by Brunton (1966) indicates that species of *Krotovia* may at times possess a distinct concentric ornament and spines arranged in concentric rows. *Dyschrestia* however, possesses coarser, rather more spaced out ventral spines than *Krotovia* and a more strongly developed interior dorsal median septum. The dorsal septum is strongly developed in both Western Australian species although weakly developed in the type species from Thailand, but, figured Thai dorsal valves appear juvenile when compared with Western Australian specimens and this may explain the discrepancy.

Jakutella Abramov (1970, p. 119, pl. 4, figs 1-17) possesses rather pronounced wrinkling—almost true concentric rugae—and a stronger concavo-convexity than *Dyschrestia*. The dorsal valve of *Jakutella* is strongly dimpled, like *Krotovia* and carries few spines. The anterior ventral spines of *Jakutella* bear short costae or radial ridges.

Janispustula Klets 1983 is of similar size to *Dyschrestia* but possesses elongate spine ridges, internal striations over the dorsal visceral disc and larger brachial ridges than *Dyschrestia*. *Lethamia*, well illustrated by

Waterhouse (1982a), is much larger than *Dyschrestia*, and although *Lethamia* possesses a dorsal septum and raised anterior adductor scars like those of *Dyschrestia* it lacks the pronounced dorsal marginal ridge of *Dyschrestia*. Spines are much finer on *Lethamia* than on *Dyschrestia*.

Dyschrestia micracantha (Hosking 1933)

Fig. 2A-O

1933 *Pustula micracantha* Hosking, p. 49, pl. 4, fig. 4a, b.

1937 *Pustula micracantha* Hosking; Raggatt and Fletcher. *Rec. Aust. Mus.*, 20: 176.

1943 *Krotovia micracantha* (Hosking); Prendergast, p. 30.

1957 *Krotovia micracantha* (Hosking); Coleman, p. 61, pl. 7, figs 16-18; pl. 9, figs 20, 21.

LECTOTYPE: GSWA 1/4970b1; Hosking, 1933, pl. 4, figs 4a, b. Chosen by Coleman (1957, p. 61).

MATERIAL, AGE AND LOCALITIES: GSWA1/4970b1 and 2, 2 conjoined crushed shells, from creek, 1.25 km west of Callytharra Springs, Wooramel River, Callytharra Formation, Carnarvon Basin. MUGDF6001-F6003, 3 conjoined crushed shells, from locality P477, measured section of type section of Callytharra Formation, Callytharra Springs, 24 m above base, collector Dr G. A. Thomas. MUGDF6004, a crushed conjoined shell, from Locality P498, as for P477, 34-38 m above base of formation. CPC1954, Pell's Range, Carnarvon Basin, 24 km northeast of Towrana Homestead, 36 m above base of Callytharra Formation; Sterlitamakian (Late Sakmarian).

MEASUREMENTS (in mm): * = lectotype

Specimen number	Hinge width	Maximum width	Ventral height	Dorsal height
GSWA1/4970b1*	14.6	17.2	13.5	12.0
GSWA1/4970b2	13.2	17.3	13.8	12.0
MUGDF6001	18.7	21.1	17.9	15.5
MUGDF6002	16.5	20.0	—	15.2
MUGDF6003	14.5	18.5	15.8	13.4
MUGDF6004	15.5	20.8	17.0	13.5
CPC1954	15.5	19.5	—	15.6

DIAGNOSIS: Large sized *Dyschrestia* distinguished by high dorsal median septum which is raised anteriorly, smaller beak and less crowded spines on the ventral valve.

DESCRIPTION: Outline transversely subelliptical; non geniculate; ventral umbo small, pointed, slightly curving over hinge line; greatest width anterior of the hinge at about midlength of shell; ventral valve moderately con-

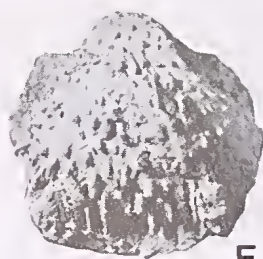
Fig. 3-A-O, *Dyschrestia colemani* sp. nov. from Wandagee Formation, Carnarvon Basin. A-E, AMF38446, holotype, shell in dorsal, ventral, posterior, anterior and lateral views, $\times 2.2$. F-I, AMF38443, ventral valve in ventral, left lateral, right lateral and posterior views, $\times 2$. J-K, AMF37579, shell with ventral valve cut away in ventral and postero-ventral views, $\times 2.2$. L-M, AMF38442, ventral valve in ventral and posterior views, $\times 2$. N, AMF37725, ventral valve in ventral view, $\times 1.6$. O, AMF37518, decorticated dorsal valve interior, $\times 2$. P, AMF37582, dorsal valve external mould with thin portions of dorsal valve remaining, $\times 2$. Q, AMF38443, ventral valve in dorsal view, $\times 2.6$.



A



B



F



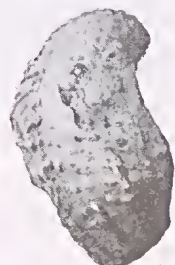
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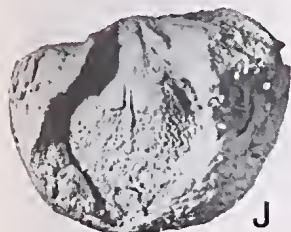
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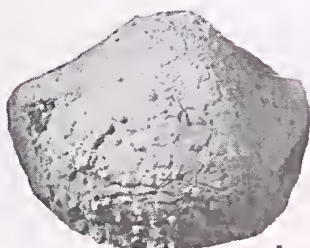
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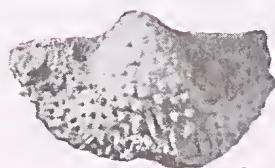
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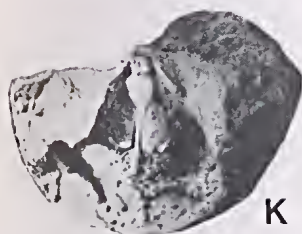
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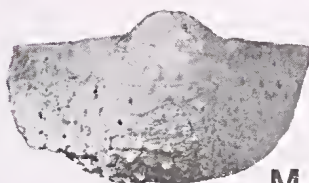
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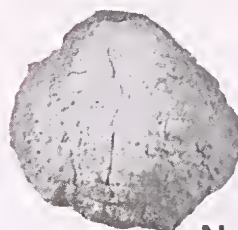
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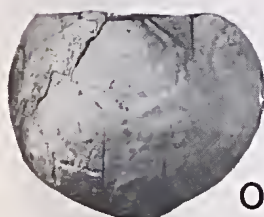
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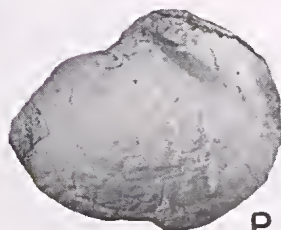
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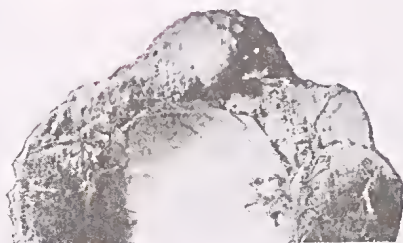
N



O



P



Q

vex; dorsal valve moderately concave; visceral cavity thin. Ventral valve covered in spines, lateral spines not distinct from visceral spines, spines arranged in concentric rows spaced usually at 1.5 mm to 2 mm intervals on anterior half of valve; successive concentric rows impart a quincuncial arrangement to the spines; dorsal spines finer than ventral spines, arranged concentrically over valve except for ears where arrangement is in two radial rows. Growth lines and delicate concentric ridges developed on ventral valve, lower and broader anteriorly; similar more pronounced concentric ornament on dorsal valve.

Ventral interior unknown. Dorsal interior with short bilobed cardinal process; muscle pads thickened and raised anteriorly; median septum arising between muscle pads, low posteriorly, narrow and high anteriorly, anterior extremely high, just under half valve length; brachial ridges weak, about two-thirds of valve length; remainder of valve covered by endospines, more pronounced at anterior extremity of valve. Pronounced marginal ridge present.

DISCUSSION: Examination of specimens not available to Hosking (1933), Prendergast (1943) or Coleman (1957) confirms that the ventral beak overhangs the hinge, that the species can be larger than previously thought and that hinge width is significantly less than maximum width of mature shells.

The species is differentiated from *D. colemani* sp. nov. and *D. spodia* by its strongly developed dorsal interior structures, notably the marginal ridge and the median septum that terminates anteriorly as a pronounced raised structure. *D. micracantha* is also distinguished by its ventral spine characteristics and a stronger development of the concentric ornament than that of the two younger species.

Dyschrestia colemani sp. nov.

Fig. 3A-Q

1943 *Krotovia spinulosa* (Sowerby); Prendergast, p. 30, pl. 4, figs 11-13.

1957 *Krotovia spinulosa* (Sowerby); Coleman, p. 65, pl. 7, figs 19-24.

ETYMOLOGY: For Dr P. J. Coleman, who has added extensively to the knowledge of Western Australian Permian Productidina.

HOLOTYPE: AMF38446, a complete conjoined shell, from the Wandagee Formation.

MATERIAL, AGE AND LOCALITIES: Nine specimens in various states of preservation. AMF37579, 403 m west of shale outcrop, north bank of Minilya River, Wandagee Formation; AMF38442, 38443, 38446 Wandagee Station, Minilya River, Wandagee Formation; AMF37563, 37564, 37578, 37582, bank of Minilya River, North West Division, Wandagee Formation; AMF37725, Wandagee Station, Minilya River, Wandagee Formation; Late Baigendzinian (Late Artinskian).

MEASUREMENTS (in mm): * = holotype

Specimen number	Hinge width	Maximum width	Ventral height	Dorsal height	Thickness
AMF38446*	12.8	17.3	15.5	13.5	8.1
AMF38443	12.0	16.5	16.0	13.2	8.8
AMF37725	—	16.1	15.6	—	—
AMF38442	15.5	19.0e	17.0+	—	—
AMF37578	—	18.0e	—	15.0	—
AMF37582	10.8+	16.0	—	12.3	—

DIAGNOSIS: Average sized *Dyschrestia* distinguished by distinctly developed median septum and muscle pads. Externally close to type species of the genus.

DESCRIPTION: Outline transversely subelliptical to circular; non geniculate; ventral umbo small, pointed, distinct; greatest width anterior of the hinge at about midlength of shell; dorsal valve distinctly concave; spines closely spaced on both valves, finer on dorsal valve; ventral lateral spines in single row in juvenile stages, double row in adult stages; remainder of ventral spines as coarse as lateral spines or at times finer; dorsal spines normally broken leaving fine pustulose bases, arranged quincuncially on most of valve except for ears where arrangement is in two distinct radial rows; growth lines poorly expressed on ventral valve, stronger on dorsal valve.

Ventral interior unknown. Dorsal interior with short bilobed cardinal process; muscle pads thickened anteriorly; median septum arising between muscle pads, low posteriorly, narrow and high anteriorly, anterior extremity low, about half valve length; brachial ridges weak, in posterior of valve, enclosing smooth floor; remainder of valve covered with endospines.

DISCUSSION: *Dyschrestia colemani* is similar to *Dyschrestia spodia* in many respects. The Thai species, however, at times is widest at the hinge (Grant 1976, pl. 22, figs 19, 20) and possesses ventral spines arranged in distinctly concentric rows (Grant 1976, pl. 22, figs 9, 29) both unlike the present species. The dorsal median septum of *D. colemani* is more strongly developed and longer than that of *D. spodia*. Comparisons with *D. micracantha* are under that species heading. The specimen from Bitauini, Timor attributed to *Productus opuntia* by Broili (1916, pl. 3, fig. 10) may be related to the Western Australian species judging from gross shell form and ventral spine pattern.

Waterhouse (1981, p. 76) considered that *D. colemani* specimens were particularly close to *Lethamia*, whereas he (1982a, p. 43) noted that the Western Australian shells are smaller, with a higher ventral umbo, more angular cardinal extremities and relatively coarser spines. Spines on *D. colemani* are certainly much coarser than on *Lethamia* and the Western Australian species possesses distinctive external dorsal dimples and distinctive dorsal adductor muscle pads. The specimen recorded by Coleman (1957) from the Cundlego Formation is also numbered T42 which is a locality of Dr C. Teichert's from the Wandagee Formation and hence the occurrence of the species from the Cundlego Formation cannot be confirmed.

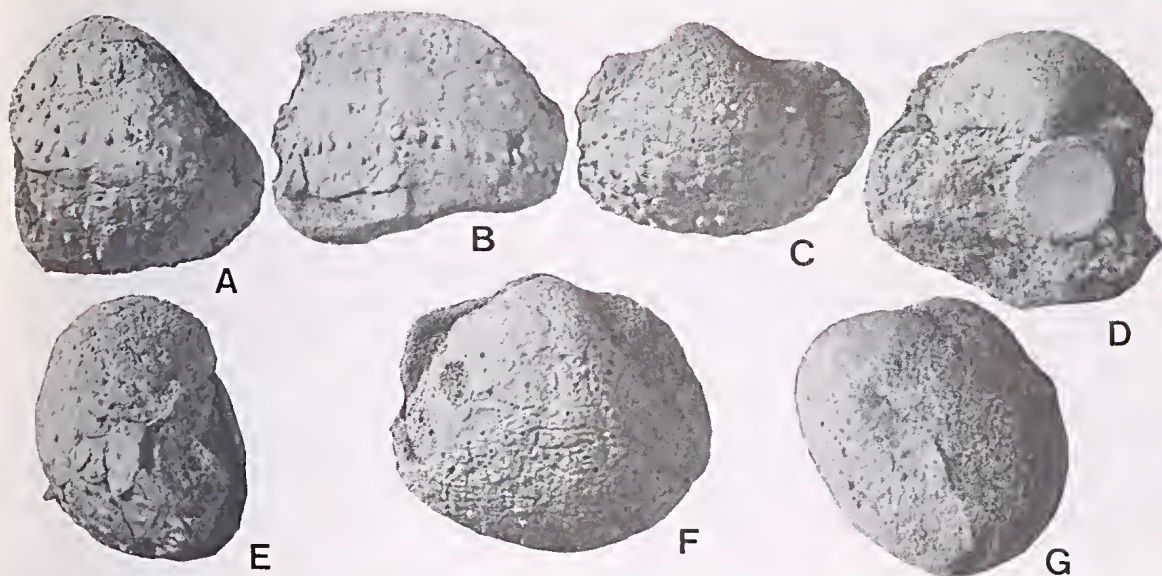


Fig. 4-A-G, *Dyschrestia* sp. from Coolkilya Greywacke, Carnarvon Basin. A-E, UWA28145b, ventral valve in ventral, anterior, posterior, dorsal and lateral views, $\times 2.5$. F-G, UWA28145a, ventral valve in ventral and lateral views, $\times 2.5$.

Dyschrestia sp.

Fig. 4

1957 *Krotovia spinulosa* (Sowerby); Coleman (*partim.*), p. 65, non. illus.

MATERIAL, LOCALITY AND AGE: 2 incomplete ventral valves, UWA 28145a and 28145b, a few hundred yards (metres) south east of Wandagee Hill, Mungadan Pad-dock, Wandagee Station (collected by Dr C. Teichert). Coolkilya Greywacke; middle Kungurian.

MEASUREMENTS (in mm): e = estimate

Specimen number	Hinge width	Maximum width	Ventral height
UWA28145a	11.5e	15.9	14.8
UWA28145b	—	15.1 +	13.6

DESCRIPTION: Circular outline; ventral valve strongly enrolled, ventral umbo small, pointed; greatest width at about midlength of shell; spines closely spaced on ventral valve (1.0 to 1.5 mm), arranged in distinct concentric rows anteriorly; spines fine with fine, circular or only slightly elongated spine bases; lateral spines in single row and, judging from bases, fine and undifferentiated from remainder of spines; ventral growth lines very weakly developed.

DISCUSSION: Although inadequate for detailed description the two specimens indicate a distinct species, differentiated from other Western Australian species by means of a highly convex ventral valve with an ornament of fine spines and fine spine bases. Details of the shell outline and the arrangement of the ventral spines may also prove specifically distinctive.

ACKNOWLEDGEMENTS

I thank Dr J. M. Dickens, Bureau of Mineral Resources, Geology and Geophysics; Dr A. E. Cockbain, Geological Survey of Western Australia; Dr A. Ritchie, the Australian Museum and Dr G. A. Thomas, University of Melbourne, for the loan of specimens in their care. Dr G. A. Thomas read an earlier version of the paper. Isabel Munro typed the manuscript and Linda Archbold assisted with photography.

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DESCRIPTION OF A NEW SPECIES OF *GADOPSIS* (PISCES: GADOPSIDAE) FROM VICTORIA

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ABSTRACT: Analysis of radiographs revealed a new species of *Gadopsis* from Victoria. The diagnostic character distinguishing the new species from *G. marmoratus*, the only described species, exhibits a range of values which does not overlap with that seen in *G. marmoratus*, even when sympatric with it. A separate species of *Gadopsis* from Tasmania, proposed by Parrish (1966), was found to be invalid when the same diagnostic characters as used by Parrish (1966) were examined.

The Gadopsidae is the only family of Australia's relatively depauperate freshwater fish assemblage which is both endemic to southeastern Australia and strictly confined to fresh water. Frankenberg (1974) considered the family to be a primary freshwater fish family, *sensu* Darlington (1957), although this view was not supported by McDowall (1981). Attempts to trace the relationships of the family have rarely reached common conclusions (see Thomson & Baldwin 1983, for a review).

Gadopsis marmoratus Richardson, the only described species, is variable in colouration and morphology, and detailed analysis of this variation may reveal a species complex. A separate species of *Gadopsis* from Tasmania was proposed by Parrish (1966) on the basis of morphological differences. His 'species' has frequently appeared in the literature under the proposed name without a formal description having been published. Despite a recommendation by Jackson and Llewellyn (1980) against its use, this *nomen nudum* continues to appear in publications (Cadwallader & Backhouse 1983), adding to the taxonomic confusion surrounding the group.

Preliminary sampling of *G. marmoratus* throughout its range revealed that specimens from King River and King Parrot Creek had distinct white margins to the outer edge of the dorsal, anal and caudal fins. The significance of this was investigated by comparing the morphometric and meristic variation within these populations with *G. marmoratus* from elsewhere in its range, in Victoria and Tasmania. Analysis of meristic variation (Table 1) revealed a new species of *Gadopsis* (described below) in King River and King Parrot Creek. The new species shares its geographic range with *G. marmoratus*, and is occasionally found in the same stream, although there appears to be a degree of habitat partitioning between them. The analysis did not support recognition of a separate Tasmanian species (Table 2).

MATERIALS AND METHODS

Live fish were collected with a portable D.C. electroshocker from shallow pools in the King River and King Parrot Creek in northeastern Victoria. Specimens were examined by using the techniques of Hubbs and Lagler (1947), except that fin ray counts include all rays, whether branched or unbranched. Pectoral ray counts were obtained by removing the fleshy skin covering the

base of the fin, to expose the rays at their origin. All other counts were obtained from radiographs. Several specimens were cleared and stained following the technique of Mahoney (1973), in order to examine dentition. Type material has been deposited in the Museum of Victoria (NMV), and the Australian Museum, Sydney (AMS).

Collections of *G. marmoratus* used in the study are as follows (numbers of individuals at each site are indicated in brackets; * indicates the collections used in Table 2): Stony Creek, 3 km upstream from junction with King River, Cheshunt, Victoria (4), 31 Oct. 1983, A. Sanger, S. Fisher and J. Rose; Kumbada Creek, 3 km upstream from junction with Stony Creek, Cheshunt, Victoria (6), 31 Oct. 1983, A. Sanger, S. Fisher and J. Rose; Kumbada Creek, 3 km upstream from junction with Stony Creek, Cheshunt, Victoria (20), 12 Dec. 1979, A. Sanger and P. Burrowes; Hurdle Creek, Bobinwarrah, Victoria (12), 6 Aug. 1979, A. Sanger and G. Gibb; Hurdle Creek, Bobinwarrah, Victoria (1), 19 Oct. 1983, A. Sanger; Chum Creek, Healesville, Victoria (15)*, 20 Feb 1981, A. Sanger; Wonnongatta River, 1 km downstream from junction with Hummfray River, near Dargo, Victoria (20)*, 21 Apr. 1980, A. Sanger and P. Burrowes; Elizabeth Creek, 2 km north of Allambee South, Victoria (19)*, 4 Feb. 1980, A. Sanger and D. Brock; Glenelg River, Victoria Valley Road, the Grampians, Victoria (7), 28 May 1982, A. Sanger and P. Murphy; Minnow River, near Lower Beulah, Tasmania (10)*, 6 Sept. 1983, R. Sloane; Lake River, 24 km south of Cressy, Tasmania (10)*, 20 Oct. 1982, A. Sanger.

SYSTEMATICS

Class PISCES
Family GADOPSIDAE
Genus *Gadopsis*
Gadopsis bispinosus sp. nov.

Fig. 1

ETYMOLOGY:

The species is named after the number of spines in the dorsal fin.

MATERIAL: Holotype, NMVA3281, female, 20.0 cm TL, coll. 15 Dec. 1979 on West branch of King River, 2 km upstream from junction with east branch of King River,



Fig. 1—*Gadopsis bispinosus*, sp. nov.; King Parrot Creek, 201 mm TL.

near Cheshunt, Victoria, 36°52'S, 146°23'E. Paratypes, NMVA3282, 5 specimens, coll. 15.xii.1979, A. Sanger and P. Burrowes, type locality. AMS I.24351-001, 6 specimens, coll. 15 Dec. 1979, A. Sanger and P. Burrowes, type locality. Other material examined, with numbers of specimens noted in brackets, King River (type locality) (8), 15 Dec. 1979, A. Sanger and P. Burrowes; King River (type locality) (6), 31 Oct. 1983, A. Sanger, S. Fisher and J. Rose; Stony Creek, 3 km upstream from junction with King River, Cheshunt, Victoria (3), 31 Oct. 1983, A. Sanger, S. Fisher and J. Rose; King Parrot Creek, 8 km downstream from Kinglake West, Victoria (13), 3 Nov. 1979, A. Sanger and C. Proctor; King Parrot Creek, 8 km downstream from Kinglake West, Victoria (7), 20 Oct. 1980, A. Sanger.

DIAGNOSIS: Differs from *G. marmoratus* in having two, or rarely one or three, spines in the dorsal fin (Table 1, Fig. 2) and prominent white fringe on the dorsal, anal and caudal fins. *G. marmoratus* has between six and thirteen spines in the dorsal fin (Table 1, Fig. 2), and lacks a prominent white fringe on the fins.

DESCRIPTION: (Holotypic values in parentheses.) A small to medium sized species; body narrow (width=0.13 of Standard Length (SL)), shallow (depth=0.19 of SL) and slightly compressed. Head narrow and slightly elongated (length=0.24 of SL); snout short (length=0.24 of Head Length (HL)); eye moderate (maximum width=0.19 of HL), inserted in upper half of head; suborbital depth large (0.53 of head depth at orbit); interorbital width narrow (width=0.21 of HL). Jaws long (length=0.40 of HL); with upper jaw extending to below the posterior half of the eye. Lips fleshy with upper overhanging lower. Teeth numerous; in premaxilla, an outer row of large conical teeth, within which there is a band of minute cardiform teeth becoming narrower towards posterior articulation; dentary similar to premaxilla; palatines and vomer bearing numerous small cardiform teeth. Two prominent rows of laterosensory pores on head; one along upper jaw margin extending upwards to behind eye; the other following lower jaw margin, extending along anterior margin of preoperculum and back towards opercular spine. Numerous smaller pores on head. Two prominent nostrils; one, halfway along snout, with fleshy tubular opening; the other, just in front of the eye, simple.

Pelvics reduced to a single fleshy bifid ray inserted jugularly (insertion point = 0.64 in HL). Branchiostegals seven; opercular spine single, with subopercular flap. Pectorals inserted laterally, below opercular spine (insertion point = 0.94 in HL), rounded, moderate in size (maximum ray length = 0.56 in HL), with fifteen to eighteen rays (16).

A single long dorsal fin (length = 0.62 of SL), inserted posterior to the level of the pectorals (insertion point = 0.28 of SL), bearing two, rarely one or three, weakly-calcified, slender spines and thirty-five to thirty-eight rays (11, 37). Anal fin long (length = 0.27 of SL), originating about half way along body (insertion point = 0.59 of SL), bearing three, strongly-calcified, stout, spines and seventeen to twenty rays (11 (one vestigial), 20). Anal and dorsal fins, when adpressed, not reaching caudal fin. Caudal fin rounded, of about thirty rays (29), half of which are branched (15). Caudal peduncle shallow (depth = 0.09 of SL) and compressed.

Lateral line, of about forty-eight tubercles, originating just above opercular spine, curving dorsally to follow dorsal profile for about the first five-eighths of the dorsal fin before descending gradually to follow midline for length of caudal peduncle.

Vertebrae forty-six to forty-nine (48), twenty-five to twenty-nine of which are caudal (27).

COLOURATION: Colouration variable, consisting typically of two uneven rows of dark brown blotches running entire length of body, extending onto dorsal and caudal fins. A third row of blotches often present, extending onto posterior half of anal fin. Brown blotches separated by paler areas; ventral surface uniformly pale from pelvic origin to anal origin. Outer edge of dorsal, anal and caudal fins white, often bordered on inner margin by an intense dark stripe. Fin rays in dorsal, anal and caudal often bright yellow in live specimens. Colour pattern more distinct in juveniles, often being obscured by intensified pigmentation in older specimens. In life, able to intensify or subdue base colouration to suit surroundings.

LIFE HISTORY: Essentially as described by Jackson (1978) and Cadwallader and Backhouse (1983), for *G. marmoratus*. Egg number varies with size of female, a 20.7 cm TL female bearing up to 350 mature eggs, 3.6 mm in diameter. Maximum TL observed, 25.7 cm, weight, 130 gm. Scales indicate fish of this size to be in their fifth year. Fish less than 10 cm TL normally juvenile (Sanger, unpubl.).

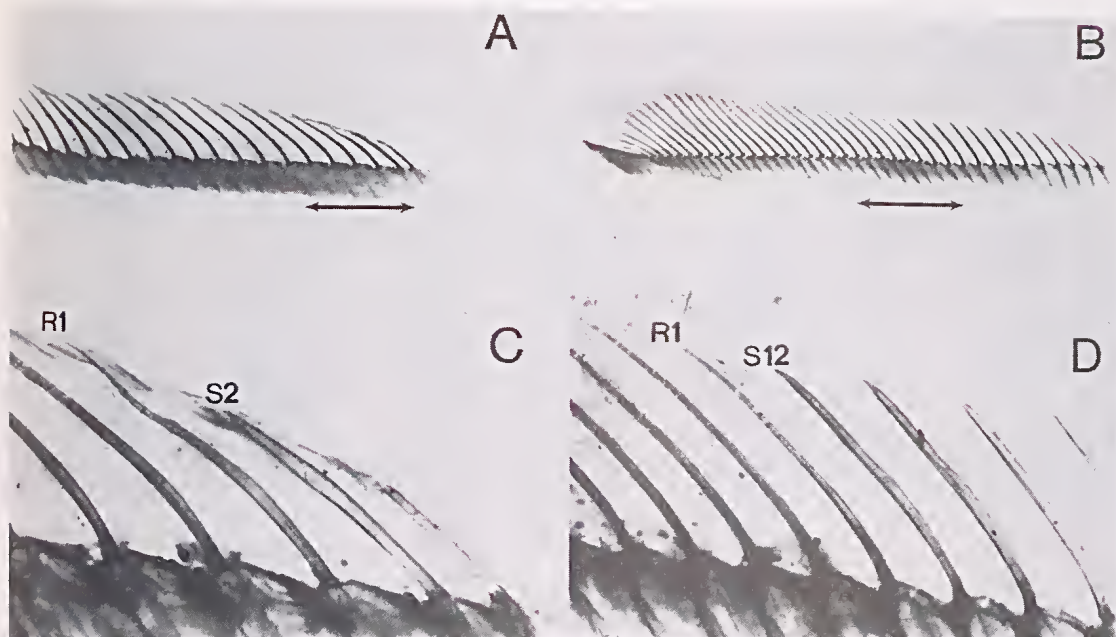


Fig. 2—Cleared and stained dorsal fins of: A, *Gadopsis bispinosus*, anterior section. B, *G. marmoratus*, entire fin. C, *G. bispinosus*, enlargement of arrowed section of A, S2 is the second spine, R1 is the first ray (note jointed appearance of rays). D, *G. marmoratus*, enlargement of arrowed section of B, S12 is the twelfth spine, R1 as above.

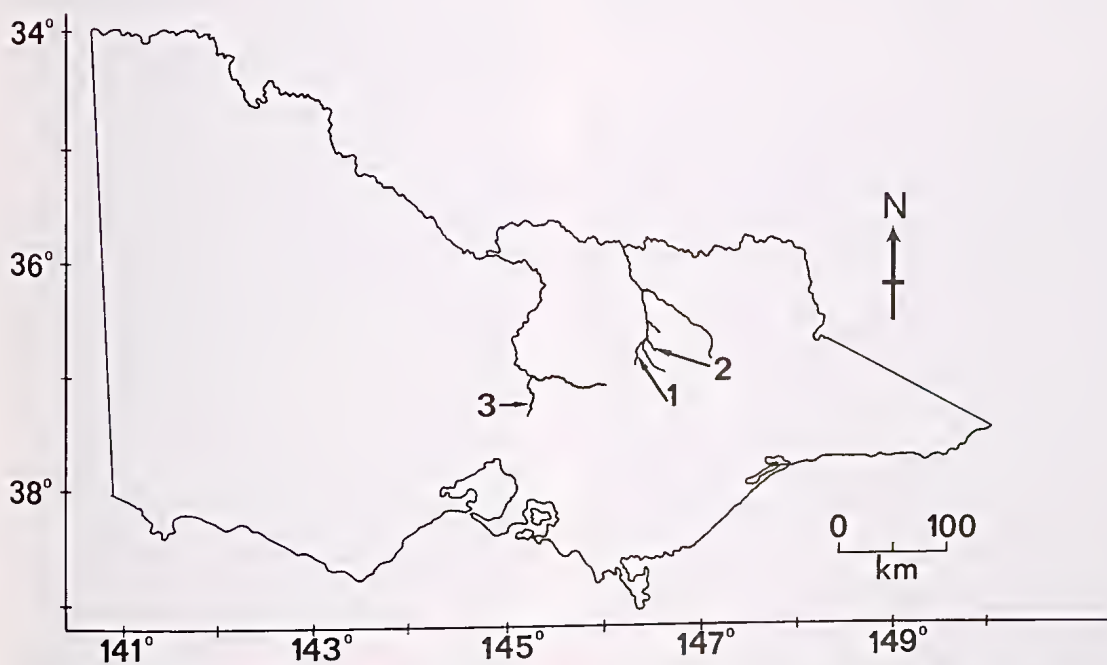


Fig. 3—Known distribution of *G. bispinosus*. 1, King River, west branch, type locality; 2, Stony Creek, near Cheshunt; 3, King Parrot Creek, near Kinglake West.

TABLE 1

MORPHOMETRIC AND MERISTIC VARIATION IN TWO SPECIES OF *Gadopsis* BASED ON THE MATERIAL EXAMINED.

Morphometric measurements other than total length are expressed as percentages of the total length. (Note the non-overlapping ranges of dorsal spine and dorsal ray counts, used to justify species separation.)

	<i>Gadopsis bispinosus</i>			<i>G. marmoratus</i>		
	Range	Mean	Std. dev.	Range	Mean	Std. dev.
Total length (TL) (cm)	116-251	173.9	34.94	101-354	207.3	62.85
Head length	17.8-22.2	19.9	1.011	18.9-25.1	22.5	1.331
Snout length	4.7-6.4	5.4	0.443	4.7-7.0	6.0	0.443
Upper jaw length	7.4-9.6	8.3	0.535	3.8-10.3	8.7	0.893
Interorbital width	3.8-5.1	4.4	0.254	4.1-6.9	5.8	0.518
Body width	9.0-12.9	10.6	1.053	9.6-14.8	12.3	1.308
Body depth	13.0-18.4	15.7	1.353	15.0-25.1	19.3	1.733
Caudal fin length	15.0-20.0	18.2	1.052	14.7-21.5	18.7	1.124
Caudal peduncle depth	6.1-7.7	6.9	0.395	6.6-9.7	8.3	0.848
Dorsal fin depth	4.3-8.0	6.1	0.871	4.6-9.7	7.4	0.892
Dorsal spines	1-3	2.0	0.243	6-13	10.9	1.416
Dorsal rays	35-38	36.9	0.772	22-31	26.6	1.447
Pectoral rays	15-18	16.5	0.701	15-19	17.7	1.402
Anal spines	3	3	0	2-4	3.1	0.378
Anal rays	17-20	18.8	0.690	16-20	18.1	1.078
Total caudal rays	28-31	29.3	0.802	27-35	30.1	1.825
Branched caudal rays	13-16	15.0	0.594	15-18	16.4	0.950
Total vertebrae	46-49	48.3	0.780	40-50	46.5	1.726
Caudal vertebrae	25-29	27.7	0.867	24-28	26.5	0.937
Number of fish measured	Morphometrics 38; Meristics 35			Morphometrics 79; Meristics 103		

DISTRIBUTION AND ABUNDANCE: Collected from the upper reaches of the King River and its tributaries, and from the upper reaches of the King Parrot Creek (Fig. 3). Common in both these streams, which have similar rocky beds and cool, clear water. Likely to be found in many of the northeastern Victorian streams which also have these characteristics.

DISCUSSION: Parrish (1966) discussed variation in dorsal spine number in populations of *G. marmoratus* from several localities throughout its geographic range. He recognised that samples from western Victoria had fewer dorsal spines than those from the rest of Victoria and from Tasmania. A sample from Violet Creek, a tributary of the Glenelg River, Victoria, showed a range of seven to nine (mean=8.2). The sample from the Glenelg River included in this study, with a range of six to nine (mean=7.6), conforms with these observations. These values, while low, partially overlap with the ranges seen for populations from other areas and, on that basis, do not warrant the erection of a separate western Victorian taxon. *G. bispinosus*, on the other hand, exhibits a non-overlapping range in this character. This is not a case of clinal variation, since *G. bispinosus* is found in sympatry with *G. marmoratus*. *G. marmoratus*, from Stony Creek, which is within 10 km of the type locality for *G. bispinosus*, exhibit a dorsal spine range of nine to eleven (mean 10.4), well within the normal range for *G. marmoratus*. The sample sites used by Parrish did not include any which were likely to have contained *G. bispinosus*, namely, clear, cool, rocky-bottomed streams in northeastern Victoria.

G. bispinosus, although sympatric with *G. marmoratus* in the upper King River, is apparently better adapted to life in clear, rocky-bottomed streams, and *G. marmoratus* to slower flowing, more turbid, soft-bottomed streams north of the Great Dividing Range. It should be noted that *G. marmoratus* occur in clear, rocky-bottomed mountain streams south of the Great Dividing Range. This distribution is analogous to that of the percichthyid genus *Maccullochella*, also found in this area (Cadwallader & Backhouse 1983). The Trout Cod, *M. macquariensis*, although rare now, was typically found in the cooler upper reaches of streams throughout the Murray-Darling system, whereas the Murray Cod, *M. peeli*, is widespread throughout the lower reaches of these streams becoming scarcer towards the headwaters. There is some evidence that these two species form interspecific hybrids in a population inhabiting Cataract Dam on the Nepean River, New South Wales (Cadwallader & Backhouse 1983). No evidence of interspecific hybrids between *G. bispinosus* and *G. marmoratus* was detected in the present study.

Whilst the past distribution of *G. bispinosus* is unknown its local abundance suggests that it may not be suffering the same reduction in numbers as has been seen in the Trout Cod. Although inhabiting trout angling waters and preyed upon by brown trout, *Salmo trutta* (Sanger, unpub.), *G. bispinosus* is the most abundant member of the fish fauna at the localities shown in Figure 3. Although three localities are hardly adequate to form an opinion, the preliminary indications are that *G. bispinosus* should not be considered a rare or en-

TABLE 2

MERISTIC VARIATION IN POPULATIONS OF *G. marmoratus* FROM TASMANIA AND FROM SOUTH OF THE GREAT DIVIDING RANGE IN VICTORIA.Based on the samples marked with an * in the lists of material. 't' value represents the result of a two-tailed Student's t-test for difference between means. Significance level, n.s. - $p > 0.01$.

	Tasmania			t	Southern Victoria		
	Range	Mean	Std. dev.		Range	Mean	Std. dev.
Dorsal spines	11-13	11.9	0.641	2.09 n.s.	9-13	11.4	0.900
Dorsal rays	24-28	26.3	1.031	1.35 n.s.	24-31	26.8	1.559
Pectoral rays	17-19	18.6	0.605	1.23 n.s.	17-19	18.7	0.499
Anal spines	3	3	0	0.96 n.s.	2-3	3.0	0.211
Anal rays	17-20	18.6	0.681	0.51 n.s.	16-20	18.7	0.795
Total caudal rays	29-33	30.5	1.100	2.60 n.s.	27-35	31.4	1.421
Branched caudal rays	16-18	16.9	0.447	0.69 n.s.	15-18	17.0	0.571
Total vertebrae	45-49	47.4	0.940	1.25 n.s.	42-50	47.5	1.170
Caudal vertebrae	25-28	26.6	0.883	0.49 n.s.	25-28	26.9	0.734
Number of fish measured		20				44	

dangered species, or, at this stage, be afforded any protection distinct from that given *G. marmoratus*.

Table 2 clearly demonstrates that the Tasmanian populations sampled belong to *G. marmoratus*. Parrish (1966) proposed a separate species on the basis of a larger number of branched caudal rays, pectoral rays, vertebrae, and lateral line pores. The first three of these characters, when examined in the present study, were not significantly different than in populations of *G. marmoratus* from south of the Great Dividing Range in Victoria, and in fact almost complete overlap in the range of values is seen. These observations should end reference to an undescribed, and apparently non-existent, Tasmanian species. A future paper will examine the question of variation within *G. marmoratus* in more detail, with reference to biochemical information as well as morphological data.

ACKNOWLEDGEMENTS

I thank Martin Gomon, Museum of Victoria, for access to X-ray facilities, Murray Littlejohn and Graeme Watson for critically reading earlier drafts of the manuscript, and the many friends and colleagues who assisted in the field. The Australian Museum Trust, and the Victorian Fisheries and Wildlife Division, contributed funds towards meeting field work costs.

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GEOMORPHOLOGY OF THE LAKE OMEO BASIN, VICTORIA

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ABSTRACT: Lake Omeo is a relic of a more extensive lake formed when a basalt flow, dated as Upper Pliocene in age, dammed the flow of Morass Creek. This larger lake is referred to as Lake Morass. Downfaulting of part of the Lake Omeo basin and upthrow of a narrow horst between the Morass Creek and Minute Creek catchments probably occurred at about the same time or later. Sedimentation of the natural overflow gap of the Lake Omeo basin during the existence of Lake Morass resulted in the basin becoming isolated from Morass Creek as the basalt flow was incised. Clay sediments over 40 m thick were deposited in the downfaulted part of the basin. Two clay lunettes to the southeast of the present lake, and material of fluvial and lacustrine origin provide evidence for alternation between wet periods when high water levels prevailed and dry periods with low water levels during which lunette building occurred. The evidence has been interpreted as indicating major changes in climate in the history of the lake. At least three lunette building phases are proposed, separated by periods of high lake levels. A palaeosol buried beneath a layer of clay of lacustrine origin is ascribed an Upper Pliocene origin.

In this paper a number of unusual features associated with the Lake Omeo basin are described and their origins are examined. An interpretation of the geomorphic history of the area and its significance in relation to Pleistocene environments in this region is proposed.

Lake Omeo, a small ephemeral lake near Benambra in the northeastern highlands of Victoria (Fig. 1), is the focus of an internal drainage basin of about 57 km². The area has a general elevation of about 750 m above sea level, but because of an extensive rain shadow produced by the Mt. Hotham-Mt. Bogong highlands to the west, the average annual rainfall is only about 630 mm. The water level in the lake fluctuates considerably, both seasonally and from year to year. It is often dry for long periods. It reached its highest level in recent times in 1956. No permanent record of lake levels is kept. The 1956 level was apparently slightly higher than the level determined during level surveys in 1960 (Fig. 2) and shown in Figs 7 and 8. Timms (1975) recorded that an earlier "lake full" year was 1896 and Bennett and Schwerdtfeger (1970) presented a collection of statements on the lake's condition over the period from 1870 to the present time. They claimed that lake full condition only occurs in association with periods of above normal rainfall. It is important to note that the term "lake full" in this context does not mean overflow into the adjacent Morass Creek drainage system.

The lake is bordered to the north by a low ridge of granite approximately 2 km long, and to the south and southeast by a low ridge beyond which is an extensive clay plain gently rising to the footslopes of the Dividing Range in the vicinity of The Sisters (Fig. 3). To the west of the lake, the basin rises through rolling to hilly topography to the watershed with the deeply entrenched Reedy Creek, and on the eastern side it is bounded by a narrow, sharply defined low ridge on which the township of Benambra is located. To the north, the

basin extends beyond the granite ridge on the lake shore as a gently rising mature landscape (Fig. 1).

Immediately to the east of the basin is the broad, alluviated valley of Morass Creek which, some 8 km to the north enters a deep gorge dissected through a flow of basalt which filled the ancient valley of the lower Morass Creek and short sections of the Gibbo and Mitta Mitta Rivers.

STRUCTURE OF THE AREA

The earliest published reference to the mode of formation of the lake appears to be a report by D. E. Thomas (1937) who noted several unusual land forms associated with the lake and suggested that it had been formed by stream capture. Thomas reproduced a map of H. S. Whitlaw (previously unpublished), showing a probable fault along the northern edge of the lake, delimiting the granite, and another fault, parallel, but about 0.8 km further north. However, he dismissed faulting as being responsible for the creation of the lake. Furthermore, he considered that the granite ridge was not related to the formation of the lake and suggested that its elevated position resulted from differential erosion.

A report by J. P. L. Kenny (1937) referred to the basalt flow in the lower Morass Creek and agreed with Thomas's suggestion that the Lake Omeo basin was isolated from the Morass drainage by sedimentation of its earlier outlet.

Hills (1975, p. 301) suggested that the lake was probably formed by back tilting of the block west of a north-south fault adjoining Benambra, with the consequent defeating of a tributary of Morass Creek. Talent (1965, p. 122) suggested that faulting which occurred during the Quaternary had played a part in its formation, and later (1969, p. 53) he described the long low ridge of sedimentary rock on the eastern boundary of the basin

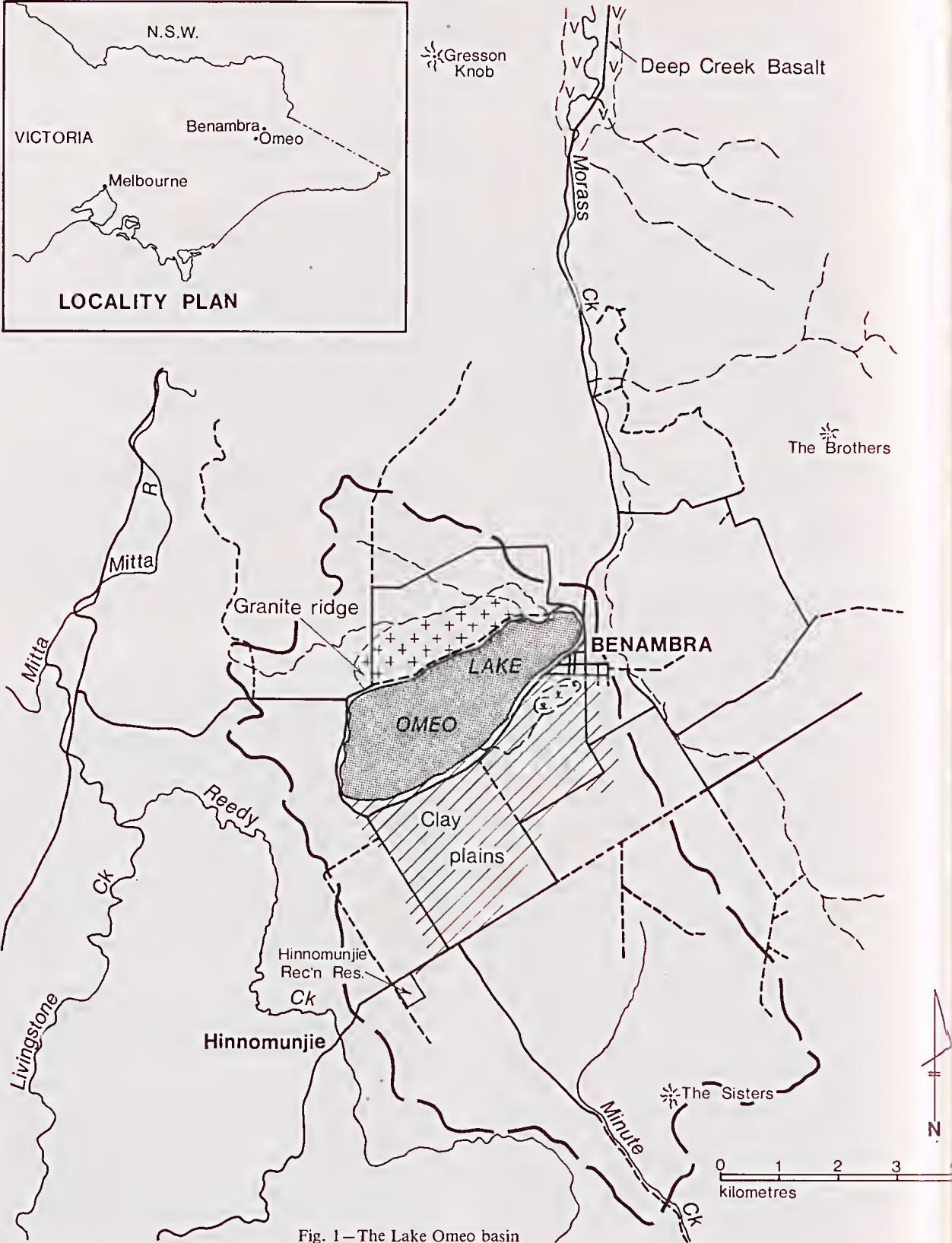


Fig. 1—The Lake Omeo basin



Fig. 2—The western end of Lake Omeo—1960.

as a small horst with its origin in the Pleistocene. He attributed damming of the lake to the horst.

Rowe (1967, p. 124) also associated faulting with the formation of the lake basin, and reported a considerable depth of alluvium in the basin so formed and the presence of two clay lunettes to the southeast of the lake, one being the lake-shore ridge (Fig. 4). The higher lake-shore or inner lunette forms a continuous ridge breached only by an ephemeral stream which includes the drainage of Minute Creek. The other lunette is south of the inner one and is lower and broken into several sections by local drainage (Fig. 5).

Both Thomas (1937) and Kenny (1937) referred to the basalt which blocked the early course of Morass Creek, and Thomas concluded that "Lake Omeo is thus a relic of a more extensive lake system". The basalt flow is referred to as the Deep Creek basalt as it is believed to have originated in the valley of that tributary of Morass Creek.

The streams have now incised the basalt to form a deep gorge and there is no ponding of water behind it except during flood flows, but before down-cutting commenced, water must have been ponded along Morass Creek for some 15 km and flooded the basin now occupied by Lake Omeo up to about the 715 m contour, the approximate level of the surface of the basalt. It is proposed to refer to this once extensive lake system as Lake Morass. Radiometric analysis of samples of the Deep Creek basalt resulted in two dates of 2.3 million years (Wellman 1974).

SUBSURFACE STRATIGRAPHY

Logs of bores sunk by a private contractor (M. Hob-

son, personal communication) in the 1940s and earlier, and of bores sunk under the supervision of the Victorian Department of Minerals and Energy in 1969, provide evidence of the subsurface materials. The locations of the Department bores are reasonably accurately known (Fig. 5) but others, except for the one in the north-eastern gap, have not been located in the field. Material from the Department bores is much disturbed but is useful in confirming the general grade of the material, its gross colour and the nature of coarse fragments.

Bores through the inner lunette, its lower slopes and the bed of the lake all indicate that grey or brown clays extend to beyond 40 m below the lake floor with occasional gravelly or stony strata, some of which contain useful water (Fig. 6). Water-bearing gravels were found at about 7.5 m below the level of the lake floor by several private bores in Benambra township, and at about 21.5 m in the clay plain south of the main lunette. Water was also found at about 33.5 m below the lake floor by Mines Department Bore Hinnomunjie No. 3. A private bore sunk on the western side of the north-eastern gap in the basin boundary struck rock at 9.1 m and a "waterbearing floor" at 18.3 m (M. Hobson, personal communication).

Water from one domestic bore in Benambra township contained 800 ppm total soluble salts at a time when water in the lake contained 2800 ppm (26/8/60) which seems to indicate a source other than a stagnant groundwater reservoir beneath the lake floor. The bore data indicate that the surface beneath the sediments is irregular and consists of granite in the north, and shales, which are present on the boundaries of the basin.



Fig. 3 — The Lake Omeo basin viewed from the southwest.

OTHER FEATURES OF THE BASIN

SANDY HIGH LEVEL BENCH

Coarse sandy sediments have been deposited by two streams which flowed into the lake from the north and west (Fig. 5). Sediments from the larger and more easterly stream extend toward the saddle in the basin boundary to the northeast, and beyond the southern edge of the granitic ridge to form a flat to gently sloping bench extending about 1.2 km along the southern flank of the ridge. The upper level of this bench is slightly below the level of the gap in the northeastern corner of the basin (Figs 7B and 8).

A 3-4 m deep excavation in the sandy bench near the northeastern corner of the lake, adjacent to the present course of the stream from the north, revealed several bands of silty material about 10 cm thick which dip in gentle curves towards the lake (Fig. 9).

The northeastern extension of the surface of the bench is clayey to a depth of more than 2 m and water accumulates in shallow depressions on it. A low levee has been constructed near the northeastern gap in the basin boundary to form a shallow dam. No such clay mantle exists over the southern part of the bench.

HIGH LEVEL FANS

Two large alluvial fans on the western slopes of the Benambra horst just south of the township (Fig. 5) have had their toes truncated at about the 700 m contour. Both fans have houses built on them.

LUNETTES

Two clay lunettes (Figs 5, 7, 8) on the southeastern side of Lake Omeo were recorded by Rowe (1967, p. 174). Several bores sunk through the inner lunette demonstrated that it consists entirely of clayey material. The results of particle size analysis of samples taken from a hole augured to 5.5 m in the top of this lunette (Fig. 11) are presented in Fig. 10. Clay contents of about 70 per cent are recorded generally below the surface 0.3 m, however, a horizon of only 45 per cent clay occurred between 3.0 m and 3.4 m from the surface. This corresponds approximately to the composition of the present surface soil and may indicate an earlier surface on which a soil formed.

The inner lunette is the higher and more continuous of the two. Its maximum height occurs near the centre of the ridge where its crest has an irregular, hummocky form (Fig. 11). It extends from the township of Benambra, where it merges with the horst of sedimentary rock, almost to the southern extremity of the lake where it gradually decreases in height to the level of the clay plain. It is breached by a small non-permanent stream which drains the greater part of the eastern half of the clay plain to the south of the lunette and includes the drainage of Minute Creek which has been channelled into a depression behind the lunette at the Benambra end. Drainage from the remainder of the southern part of the basin enters the lake at the southern end of the lunette.



Fig. 4—The inner lunette viewed from the south. The much reduced outer lunette can be identified by the rise in the left-hand fence line.

Another noteworthy feature of the inner lunette is the presence, towards its eastern end, of a flat to gently concave bench sloping up from the lake side to the crest (Fig. 8). The flat part of this bench is at approximately the same level as the tops of the sand deposits on the northern shore.

The outer lunette is broken into three short sections by drainage channels at the general level of the clay plain between the two lunettes. The southwestern section is the highest and the lowest is the eastern section. There is no obvious evidence of this lunette having extended east of a line extending southeast of the breach in the inner lunette.

The general level of the clay plain to the south of the inner lunette is some 4 m higher than the floor of the lake as shown in Fig. 7A. A number of crescentic depressions to the south of the two main lunettes may indicate the presence of other low mounds of lunette-type origin. Level traverse C, (Fig. 7A) shows a rise in level to the south of the outer lunette which may be the truncated relic of another lunette.

BEACHES

Several beaches are cut in both the southern and northern shores of the lake. Two main beaches are shown in Fig. 7A and 7B. Each is gently sloping and up to 20 m wide and has abundant limestone gravel on its surface. Numerous other lap-lines exist on the lunette shore. The recent highest water level (circa 1956-57) coincides with the lowest of the prominent lunette-shore beaches on the southern side of the lake.

On the northern shore, which is dominated by the sand deposit described above, the remnant strandline morphology is less well preserved than on the clayey southern shore.

THE CLAY PLAIN

To the south of the inner lunette, and extending from the foot of the Benambra horst in the east to near the Hinnomunjie Recreation Reserve in the southwest, is a flat to gently sloping plain. The regularity of its surface is broken only by the low ridges of the remnants of the

outer lunette and shallow drainage depressions including Minute Creek and the swamp south of Benambra township. Its southern margin is indented by low bedrock ridges which extend north from the slopes of the Divide which forms the southern boundary of the basin (Fig. 1). The material forming the plain is clay, as indicated in a number of holes augured to examine the soils.

POSSIBLE OVERFLOW GAPS IN THE BASIN BOUNDARY

Dumpy-level traverses were run to several low gaps in the eastern boundary of the basin. The gap in the northeastern corner was the lowest with a relative level (above a local benchmark established for the purpose) of 34.1 m, but the gap to the southeast of Benambra school was only slightly higher, 34.3 m. The cross-sections of the northeastern gap (along the road) and school gap are shown in Fig. 12A, B. The contour map shows all these gaps as being below 700 m elevation (Fig. 5).

SOILS

SOILS OF THE CLAY PLAIN

Examination of soils by auguring in the southwestern corner of the clay plain, near the Hinnomunjie Recreation Reserve has revealed the existence of a soil buried beneath dark clayey sediments (SCA Profile 550 Appendices 1, 2).

The upper soil is generally a very dark brown to black clay, about 30 cm thick. It has a clear to abrupt boundary with a lighter coloured and lighter textured horizon which is the A-horizon of the buried soil. The buried soil is a duplex soil (Northcote 1979) with an abrupt and wavy boundary between the A-horizon and a heavy clay B-horizon varying from about 6 cm to 10 cm below the buried surface. The upper B-horizon of the buried soil has weak structure but below 55 cm the structure is strongly developed with 1-2 cm blocky to prismatic peds which are coated with thick black cutans.

SOILS OF THE LUNETTES

The soils on the inner lunette are dark clays with a

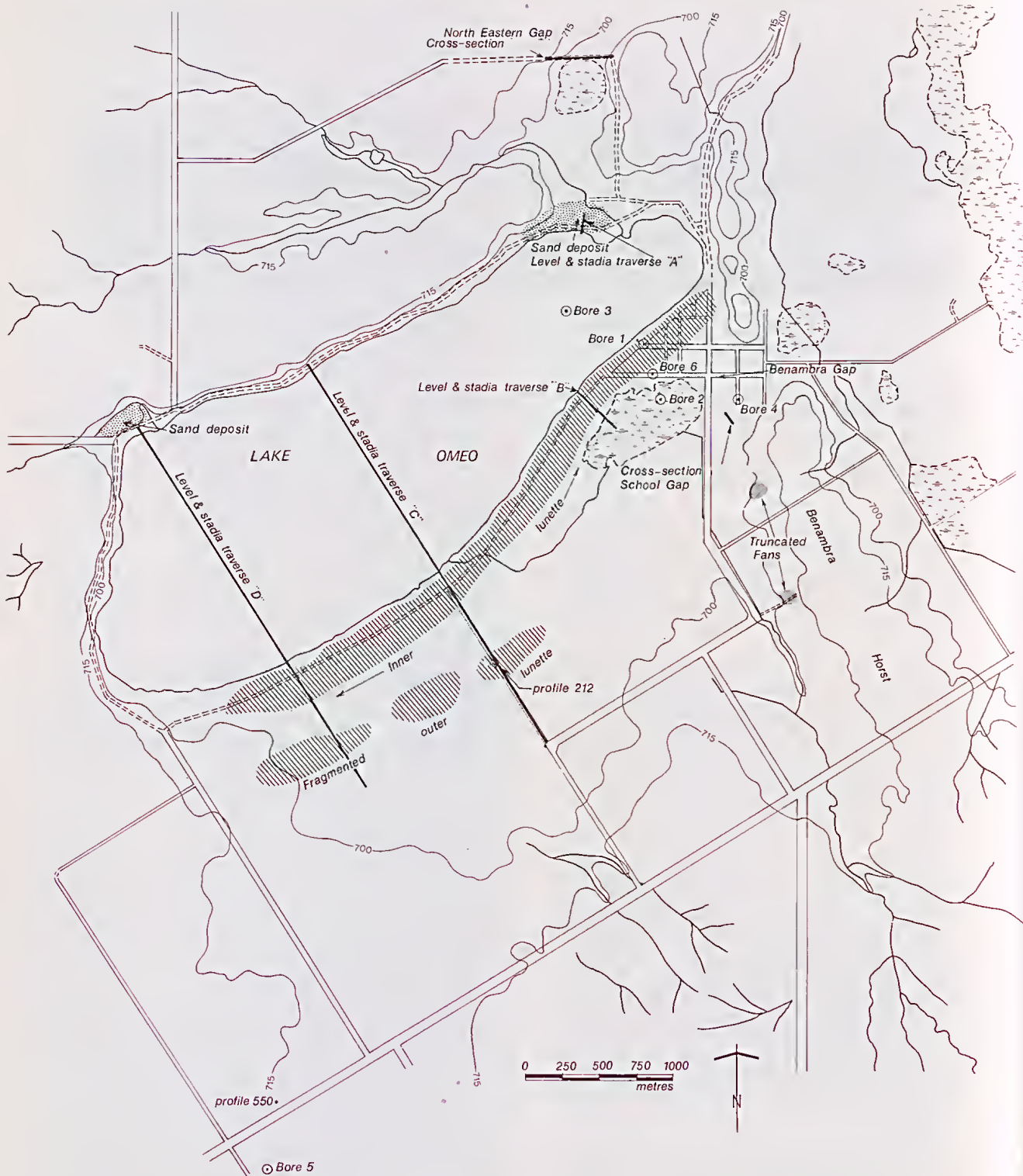


Fig. 5—Features associated with the Lake

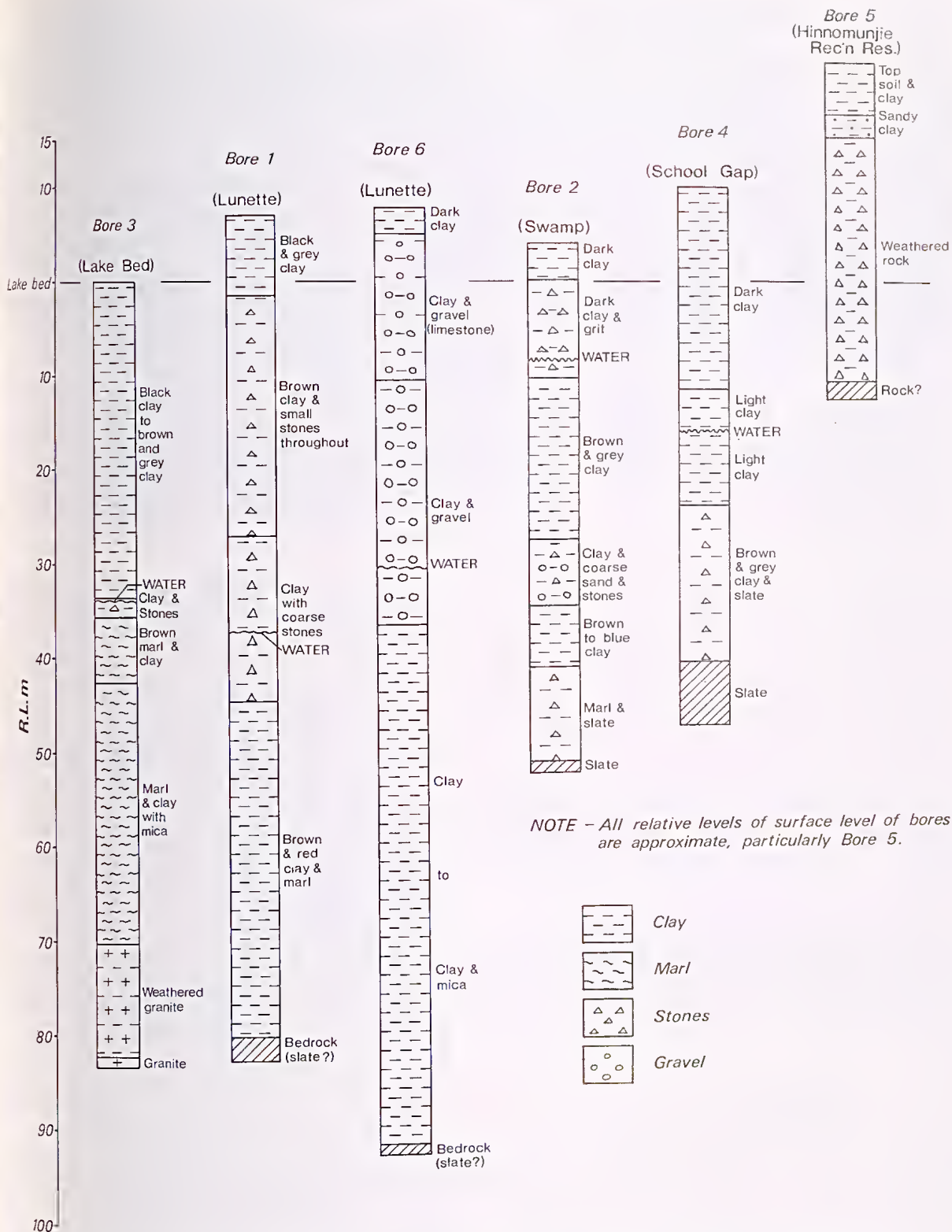


Fig. 6—Diagrammatic representation of bore logs from Lake Omeo. (Data from Department of Minerals and Energy, with permission).

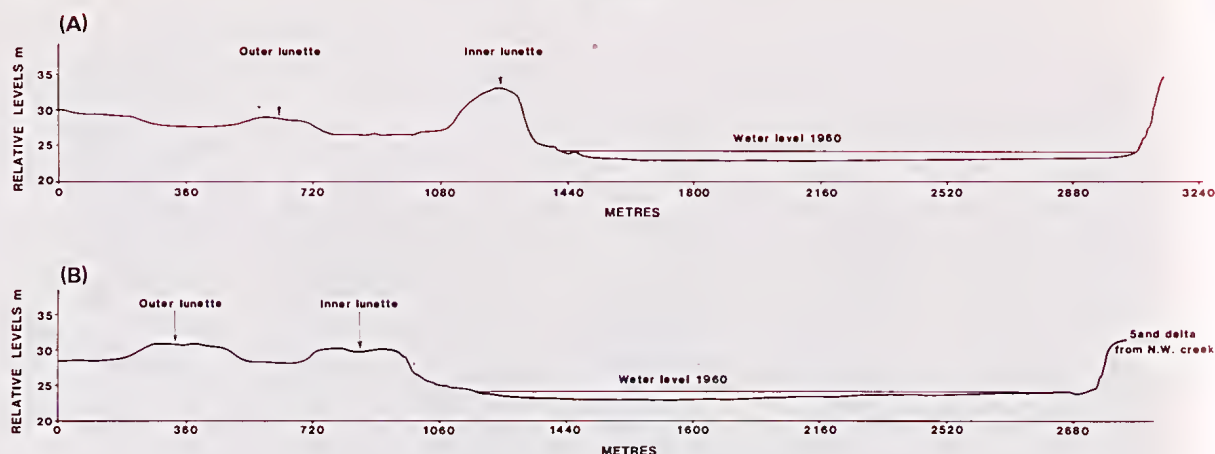


Fig. 7—A, Level and stadia traverse C
B, Level and stadia traverse D

strongly developed structure at the surface, becoming an olive-grey heavy clay with depth. They are neutral to slightly alkaline in the surface but become alkaline in the subsoil where free lime, either as soft or small hard concretions, is usually present.

A soil on the outer lunette (SCA Profile 212 Appendix 1) has a fine sandy clay loam to fine sandy clay surface which is strongly acid to acid and which at 15 cm depth abruptly overlies a dark clay which is slightly acid to neutral. The clay content increases until below depths of about 30 cm it remains consistently high (75 per cent) and the reaction rises to very alkaline (pH 8.4) (Appendix 2). Hard limestone concretions up to 10 cm diameter are present at about 70 cm depth. The surface 15 cm appears to be a separate layer of more sandy material.

THE SOIL IN THE NORTHEASTERN GAP

The soil in the bottom of the small dam is a dark cracking clay. Just beyond the low wall of the dam the soil is a weakly differentiated clay loam to clay to 80 cm below which is a dense clay with 1-2 cm blocky peds to 200 cm.

OTHER SOIL INFORMATION

The soils were examined along the road reserve which extends to the northeast of the site of the buried palaeosol. The surface soils on the sloping sides of the valley of Minute Creek and the Benambra horst (up to approximately the 715 m contour) were found to be

conspicuously darker and to greater depth than soils above that level.

INTERPRETATION OF DATA: THE SEQUENCE OF EVENTS

FORMATION OF THE LAKE OMEO BASIN AND LAKE MORASS

The regional landscape was of relatively low relief prior to the tectonic events which led to the formation of the basin. There are numerous relics of this landscape in the region—the low gaps in the Dividing Range at Tongio Gap and Cassilis Gap and small plateaux such as McMillans Lookout, and many of the hilltops between Omeo and Benambra.

Crohn (1950) described a fault along the Livingstone Creek which may have been a major cause of regional stream rejuvenation. The fault on the southern edge of the granite ridge which forms the northern shore of Lake Omeo (Thomas 1937), and the formation of the Benambra horst (Talent 1965, 1969) may also have occurred at this time. Talent (1969) proposed a Pleistocene age for this latter event. These faults formed the Lake Omeo graben with a down throw of some 70 m in the northeastern corner.

The blocking of Morass Creek by the Deep Creek basalt was more or less contemporaneous with or predated the rejuvenation of the regional drainage system as the landscape upstream has escaped the re-

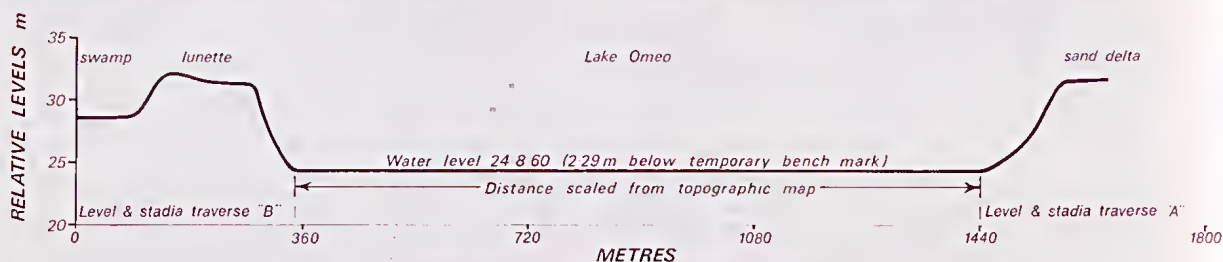


Fig. 8—Level and stadia traverses A & B.



Fig. 9—The sand deposit in the northeastern corner of the lake. Note the darker bands of silt.

juvenation. Radiometric dating of the basalt (Wellman 1974) places this event in the Upper Pliocene (2.3 my). Plugging of Morass Creek by the basalt resulted in the formation of an extensive lake, for which the name Lake Morass is proposed.

EFFECTS OF LAKE MORASS UP TO THE FORMATION OF THE MORASS CREEK GORGE

The great depth of clay revealed by the bores in and adjacent to Lake Omeo indicates a long period of accumulation during which the waters of Lake Morass flooded the basin to approximately the 715 m contour. However, during this period there was at least one drier period when there was little or no water in Lake Omeo. The presence of "stones" recorded in the bore logs (as distinct from "gravel", which in some instances at least are secondary carbonate nodules) indicates fluvial transport. Further clay deposition followed, indicating a return to high lake levels.

Several low gaps between Lake Morass proper and the Lake Omeo basin were also sites of clay deposition (see Bore 4—School Gap, Fig. 6). However, the lowest gap is that in the northeastern corner of the basin and its cross-section (Fig. 12A) seems to indicate that it did not carry eroding flows after the final decline of the level of Lake Morass, i.e. after Lake Omeo finally became independent of the Morass Creek drainage system. This does not deny the possibility that at some intermediate stage, eroding flows may have passed between the lakes, most probably flowing into Lake Omeo because of the larger catchment of the Morass. If this happened, sedimentation in the gap or wave levelling as the waters subsided would have tended to smooth the gap profile.

The coarse sandy deposit which extends beyond the northeastern end of the granite ridge is a delta formed by deposition in the high level Lake Omeo from the small stream draining the northwest of the basin. The thin gently dipping silt bands within the deposit mark changes in the depositional regime, probably periods of less erosion in the catchment when lacustrine deposition predominated over fluvial deposition by the stream.

The interpretation of the formation of Lake Omeo by sedimentation of the overflow gap (Kenny 1937) is therefore partly correct. If the small stream which drains the area north of the granite ridge had not been diverted to the south of the gap by its own sediment, it is probable that the northeastern gap would have been gradually lowered as the level of Lake Morass was reduced, and the waters of the Lake Omeo basin may have now drained through it.

There is, however, evidence of lacustrine rather than exclusively fluvial sedimentation in the northeastern gap. The soils in the bed of the dam in the gap are dark cracking clays and a hole augured just northeast of the dam wall encountered heavy, strongly pedal clay between 80-200 cm. This means that much of the sand deposit exposed on the lake shore postdates the isolation of Lake Omeo from Lake Morass or at least that the present day bench was cut after isolation.

Several alluvial fans on the western slope of the Benambra horst and at least one on the granite ridge have been truncated at about the level of the 700 m contour. No detailed levelling has been carried out on these features but it seems probable that the truncation was effected when the lake was below the maximum level of about 715 m. It is therefore proposed that the fans were

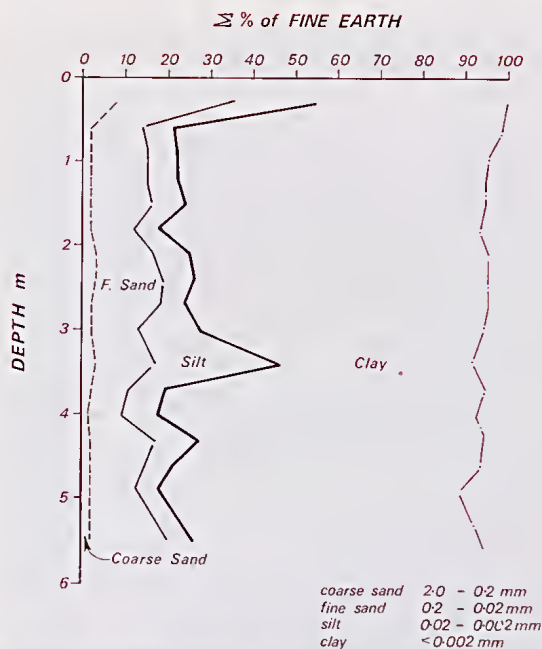


Fig. 10—Particle size analysis of a soil profile on the crest of the inner lunette.

formed during a relatively dry period (low lake levels) when surface erosion was prevalent, possibly related to a period of “stone” deposition on the basin floor. The fans were subsequently truncated upon the refilling of Lake Morass. That this was at about the 700 m level indicates that, by that time, the Morass Gorge had been incised some 15 m below the top of the basalt.

The Morass Creek gorge was eventually cut through the basalt and Lake Morass was drained. Until recently the course of the creek for several kilometres above the basalt was very swampy but it has now been artificially drained.

THE LAKE OMEO BASIN AFTER ISOLATION FROM LAKE MORASS

There is a lack of evidence to indicate what happened between the isolation of Lake Omeo and the formation of the “outer lunette”. Low lake levels and conditions favourable for lunette formation must have prevailed for a considerable time to produce this lunette which has a base about 300 m across (Fig. 7B) at its widest. This lunette marked the southeastern shore of a lake, which may have been formed in that area by further slight down faulting of the graben.

Bowler (1980, 1983) has described the conditions required for lunette building. He rejects the effect of ice crystals in producing the clay aggregates on the basis of the lack of supporting evidence from Lake George. However, he emphasises the importance of salts, especially chlorides in the formation of clay aggregates.

The inner lunette has similar width of base to the outer lunette, and has for much of its length the typical dune form as is shown in level traverse C (Fig. 7A). The presence of pairs of lunettes such as this has been reported by others (Stephens & Crocker 1946, Campbell 1968) although no single explanation appears to satisfy all cases. In this case it seems likely that slight down faulting of the graben may have caused the ephemeral lake to contract, thus creating a new shore just north of the original lunette.

The size of the inner lunette is also such that a considerable period of lunette building was involved and the floor of the lake was eroded to some 4 m below the general level of the plain between the two lunettes.

A period of higher lake levels interrupted lunette building, and wave action truncated both lunettes to the form shown in Fig. 7B. The gentle northerly dip of the line of accordance across the lunettes on this cross-section suggests that further downward movement on the northern edge of the graben may have occurred subsequently.

Some reshaping of the surface of the sand delta by wave action is evident in level traverse B (Fig. 8) and from the extension of this bench along the northern shore of the lake at the foot of the granite scarp. The level of the bench is approximately 3 m below the level of the northeastern gap (the “overflow gap”) which indicates that the high water level responsible occurred at a time when Lake Omeo was independent of the Morass Creek drainage system. However, it is accordant with the tops of the two lunettes (Fig. 7B) at the western end of the lake and with the bench at the eastern end of the inner lunette (Fig. 8).

Return of drier conditions led to resumption of lunette building on the inner lunette.

The bench at the eastern end of the inner lunette is, on present levels, at about the same level as the tops of the two lunettes at their western ends (Fig. 7B). However, the bench on the eastern end of the outer lunette is about 2 m lower and dips slightly more steeply than those at the western end (Fig. 7A).

The further down-faulting proposed above could have produced these differences. However, as the bench at the eastern end of the inner lunette is still at about the level of the benches at the western end (31 m), and this is

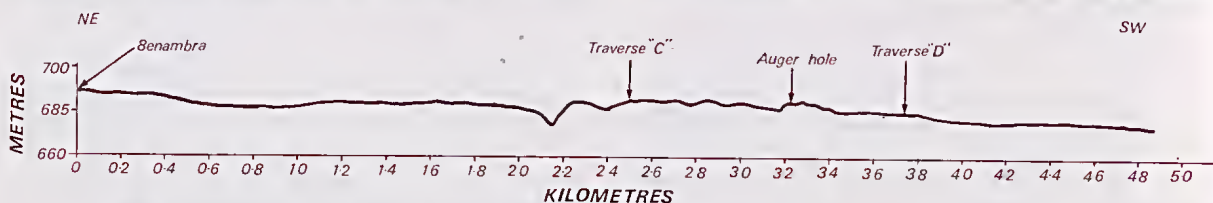
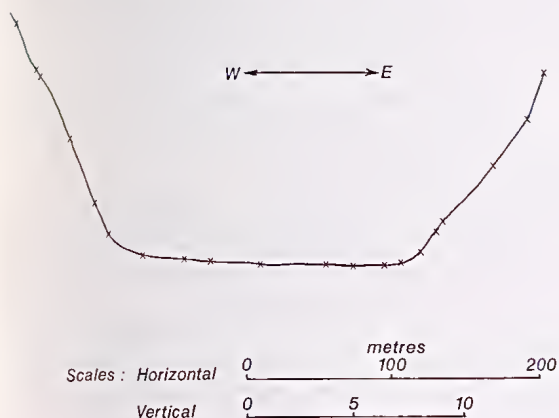


Fig. 11—Traverse along the road on the top of the inner lunette. (Aneroid barometer and car odometer.)

(A) Cross-section of north-eastern gap of Lake Omeo
(Lowest point Relative Level 31.1m)



(B) Cross-section of school gap of Lake Omeo
(Lowest point Relative Level 34.3m)

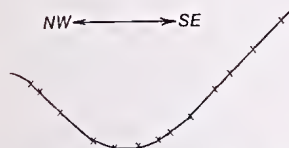


Fig. 12—Cross sections of the lowest gaps in the basin's boundary.

in accord with the bench on the sand deposit on the northern shore, it is proposed that another period of high lake level occurred and further wave shaping of the emergent inner lunette resulted. A period of lunette building between the two high lake phases, as above, was necessary to build the inner lunette above the level of the truncated eastern end of the outer lunette. The sand delta and bench would also have been reshaped by the second phase of high lake levels.

Return to drier conditions and renewal of lunette building mainly in the centre of the inner lunette, resulted in building up clay bodies with dune-form sections and an irregular crest line (Fig. 11). The small low ridge on the northern edge of the inner lunette on level traverse D (Fig. 7B) and the more typical lunette form on level traverse C (Fig. 7A) are the result of this renewed activity.

The particle size distribution study of the profile in the crest of the inner lunette shows a marked break in the sedimentary pattern some 3.5 m below the surface. This is at about the level at which the lunette would have been truncated if the hypothesised high lake level is correct.

The bench at the eastern end of the inner lunette appears to mark the last high water level in Lake Omeo. Several small beaches were identified by fairly detailed levelling close to the water level in 1960. These, no doubt, marked brief periods of climate wetter than that of the present.

INTERPRETATION OF THE SOILS EVIDENCE

The buried duplex soil near the southwestern edge of the clay plain is a very well differentiated soil and the overlying layer is clearly of different material. The uniformity and fine texture of this material (Appendix 2) suggests a lacustrine origin. The 715 m contour is drawn close to the site but may not be very accurately placed; however, the site appears to have been close to the margin of Lake Morass when at its highest level. The extensiveness of clay cutans on the voids in the buried soil and particularly their thickness on the structural units of the buried B-horizon suggest a long and/or efficient leaching of clay from the mantling sediments and periodic drying to form the cracks. This is consistent with shallow lake conditions where periodic inundation and drying out occurred.

It is not possible that the waters of the independent Lake Omeo reached this level because the natural overflow gaps are much lower. It is therefore proposed that the buried soil was at the surface prior to the formation of Lake Morass. It is thus a palaeosol dating from the Upper Pliocene. The 2.3 million year age for the basalt (Wellman 1974) provides a valuable dating for this soil.

The soil on the outer lunette is also two layered, however, that site is within the reach of high water in the independent Lake Omeo. The fine sandy texture of the surface layer is consistent with the washing of the finer particles from the characteristically clayey lunette material by wave action.

The large (10-15 cm), dense (marble-like) lime concretions at relatively shallow depth (70 cm) in the outer lunette are of interest. They are clearly the result of a long period of accumulation. Whether they formed during the lunette building phase when they may have been within the local watertable zone, or after the initiation of the inner lunette or at a later stage still cannot be determined. There is probably still a localised watertable near the surface of the clay plains despite the lake floor being up to 4 m lower, because of the poor drainage and heavy texture of the material. Therefore it is likely that carbonate accumulation is still occurring.

Bowler (1980, 1983) has argued the significance of the presence of a watertable at shallow depth in the formation of clay lunettes. It therefore seems very likely that the concretions started to form at the top of the watertable when the outer lunette was being formed. Careful sampling of carbonate from the centre of the larger concretions may provide material for C^{14} dating which could indicate the age of commencement of accumulation.

THE CLIMATIC SEQUENCE

The analysis of late Pleistocene climatic fluctuations in the Lake George basin of NSW (Coventry 1976) suggests that lower temperatures than at present, which reduced evaporation, were of more importance in establishing high lake levels than increased precipitation. In fact reduced precipitation may have occurred at the same time. Thus, the use of the terms wetter or drier

in this discussion refers to the relative balance between precipitation and evaporation and is relative to the current long term balance. In his study of mallee landscape development Bowler (1980) related the dune/lunette building phases to glacial periods and high lake levels to interglacials. Thus, the drier periods are assumed to have been colder and with lower precipitation whereas the wetter periods could have been so because of higher precipitation, lower evaporation or combinations of both.

The existence of fluvial material (stones other than calcareous concretions) within the clayey lacustrine sediments of the basin indicates that at least during one prolonged period during the existence of Lake Morass, the flooding of the Lake Omeo basin was periodic at most. There is a zone roughly 30–40 m below the lake bed in which stones are present in both Bores 1 and 3, and at similar depth in Bore 2 coarse sand and stones are present. Therefore at a time corresponding to about halfway through the period of lacustrine sedimentation a drier climate than that which kept the basin flooded prevailed for long enough to enable stones to be deposited through approximately 10 m of the sedimentary sequence. The fans on the western slopes of the Benambra horst may have formed at this time also.

At some period after the isolation of the Lake Omeo basin from the Morass Creek drainage, the climate was suitable for lunette building. The size of the outer lunette indicates a long period of such climate. Building of the inner lunette would have taken as long again. It has been proposed that the presence of two lunettes was caused by a change in the lake shape due to fault movement, and it is possible that the drier climate spanned the two lunette building periods; however, it is also possible that two major cycles of wet/dry conditions were involved.

The benches cut across the western ends of the two lunettes required a high level and a wetter climate. Return to the drier climate required for lunette building followed which resulted in further addition to the inner lunette.

Another lake-full period with wetter climate occurred during which the bench on the northern sand deposit and the bench at the eastern end of the inner lunette were shaped. A relatively short period of lunette building followed, resulting in redevelopment of the typical dune form in the central part of the inner lunette.

Subsequent climates have not caused sufficient change in geomorphic processes to have left clear evidence in the features of the basin. The sequences of small beaches on the lake side of the inner lunette indicate successively lower stands of lake level which may have occurred during the drying out after the last lake-full period. However, these beaches are still clearly defined and are probably relatively young. Therefore, a more recent period of higher than current lake level, but not as high as the major fillings referred to above is proposed. This could have resulted from a short period of wetter climate.

The present climate is such that in general the annual precipitation is less than evaporation so that the lake

only contains water in those infrequent periods when higher than average rainfall occurs over several years (Bennett & Schwerdtfeger 1970). Sufficient rainfall occurs for complete vegetative ground cover, even when there is insufficient to put water in the lake, so there is currently no evidence of lunette building.

A highly generalised diagrammatic representation of the climatic variation indicated by the land forms of the basin is presented in Fig. 13.

Bowler's (1980) analysis of palaeohydrology in the mallee regions of NW Victoria and SW New South Wales resulted in the postulation of several cycles of drier dune/lunette building periods and wetter periods when high lake levels prevailed. He is able to ascribe approximate ages to the various phases by means of radiocarbon dating of material representing the more recent events and by correlation of the inferred palaeohydrologic conditions with glacial/interglacial chronology established elsewhere and the palaeomagnetic reversal for the earlier events.

The only absolute date available from this study is that of the basalt flow (2.3 my: Wellman 1974) which marks the starting point for the features described in this paper. Thus the Lake Omeo land forms come within the age scale proposed by Bowler for the Mallee areas, and as he considers that the climatic changes involved were of global significance it is tempting to try to correlate the proposed climatic variations interpreted from the Lake Omeo evidence with those proposed by Bowler for the Mallee.

The simplest interpretation is to relate the high beaches on the inner lunette to the cliffing at Lake Frome and Lake Tyrrell (10 000 yr BP), the last lunette building phase to the Mungo–Zanci Arid Period (25 000 to 15 000 yr BP) and the last major lake full period to the Mungo Lacustral Phase (50 000 to 25 000 yr BP.). However, the small magnitude of the younger features at Lake Omeo may mean that these three periods should be shifted back one cycle to correspond with the last two lake full periods, with the intervening lunette building period. This interpretation is presented in Fig. 13.

CONCLUSIONS

Although considerable evidence of the sequence of development of the natural features of the Lake Omeo basin is presented, there are many gaps and no doubt more field work would help to overcome this. Some of the hypotheses of renewal of down faulting and the shaping of the lunettes and other sedimentary land forms by high levels in Lake Omeo depend on the precision of the level traverses. Additional detailed levelling would be needed to check some of these. However, in general, differences in levels required to support the hypotheses are of the order of 5–20 m. The existing level surveys are well within that order of accuracy, but in some instances contour mapping has had to be relied upon and this presents problems in an area of such low relief. Even so, the degree of confidence in their level of accuracy seems reasonable.

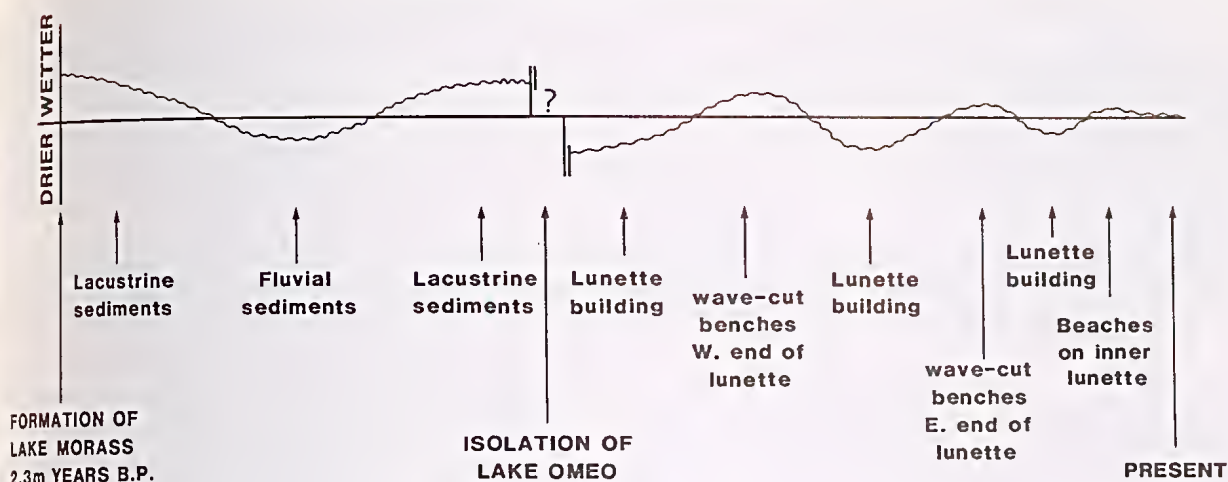


Fig. 13—Generalised representation of climatic variation as indicated by land forms of the Lake Omeo basin.

The climatic sequence proposed, though very broadly sketched, reflects patterns of change proposed by others (e.g. Bowler & Hamada 1971).

The significance of the evidence of the antiquity of some of the soils requires further consideration. Pedologists have generally agreed that the well differentiated duplex soils are very old but the extreme age indicated here is of great interest. The geomorphic-pedogenetic frame work proposed in an area to the north (van Dijk & Rowe 1980) supports the existence of soil materials of considerable age in the present day landscape, however, the inferred age of the buried soil from Lake Omeo is extreme. The area presents a unique opportunity where a soil of great antiquity has been preserved from erosion while elsewhere in the highlands there was substantial landscape dissection and surface stripping.

Of the period between the final isolation of Lake Omeo from Lake Morass and the building of the outer lunette, there is no geomorphic evidence. Nor is there any indication of the length of time required for lunette building. Radiocarbon dating of the marble-like concretions from the outer lunette may not be capable of indicating their true antiquity for they may well have originated beyond the range of the technique.

Because the Lake Omeo Basin is an area of internal drainage and has escaped the rejuvenation which has affected much of the region, many fossil features are preserved. It could still be a most fruitful area for further study. Radiometric and palynologic studies would no doubt prove worthwhile.

ACKNOWLEDGEMENTS

Field work on this study extended over a number of years and in that time the various level surveys have been carried out with the able assistance of A. S. Rundle, J. C. W. Langford and R. Smith for which I am thankful. Constructive and encouraging criticism by Dr J. M.

Bowler of the A.N.U. of early drafts of the manuscript were greatly appreciated.

Most of the field work and all of the typing and drafting of figures for the paper were carried out at the Soil Conservation Authority of Victoria; the willingness of the Authority to promote this study and approval for publication of the paper are gratefully acknowledged.

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APPENDIX 1 MORPHOLOGY OF SOIL PROFILES

Description of two-layered soil from clay plain near Hin-nomunjie Recreation reserve.

SCA Profile No. 550

0-10 cm	very dark brown (10 yr 2/2 moist) clay; moderate, 0.5-2 cm subangular blocky structure; clear smooth boundary
10-30 cm	black (10 yr 2/1 moist) light clay; weak to moderate, 0.5-2 cm subangular blocky structure; clear smooth boundary
30-36 (40) cm	light brownish grey (10 yr 6/2 moist) loam; apedal; abrupt wavy boundary
36(40)-55 cm	mottled black and dark yellowish brown (10 yr 2/1; 4/4 moist) heavy clay; weak, 2 cm blocky to prismatic structure; gradual boundary
55-82 cm +	mottled black and olive brown (10 yr 2/2; 2.5 y 4/4 moist) heavy clay; strong, 2 cm blocky to prismatic structure

SCA Profile No. 212

0-7 cm	black (10 yr 2/1 moist) fine sandy clay loam; moderate, 0.5-4 cm angular blocky structure; clear smooth boundary
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7-15 cm	black (10 yr 2/1 moist) fine sandy light clay, moderate, to strong, 0.5-4 cm angular blocky structure; clear smooth boundary
15-30 cm	mottled black and dark yellowish brown, heavy clay; strong, 0.5-1 cm angular blocky structure; weak clay cutans; occasional 1 cm carbonate concretions; clear smooth boundary
30-60 cm	mottled black and dark yellowish brown, heavy clay; strong, 1-5 cm blocky peds arranged in columns; well developed clay cutans; occasional 2 cm carbonate concretions; clear wavy boundary
60-100 cm +	mottled olive brown and black, heavy clay; strong, 0.5-2 cm subangular blocky peds weakly arranged in columns; well developed clay cutans; carbonate concretions up to 25 cm common—decreasing below 100 cm.

APPENDIX 2 PARTICLE SIZE ANALYSIS OF SOIL PROFILES

(1) SCA Profile No. 550

	Sand			
	Coarse	Fine	Silt	Clay
0-10 cm	5	29	22	44
10-20 cm	10	35	21	31
20-30 cm	12	38	24	27
30-40 cm	12	43	28	17
40-55 cm	5	18	9	66
55-75 cm	6	25	15	54

(2) SCA Profile No. 212

0-7 cm	11	36	17	27
15-30 cm	6	22	6	58
120-150 cm	1	11	9	74

SYSTEMATICS, ANATOMY AND BORING MECHANISMS OF THE ROCK-BORING MYTILID BIVALVE *BOTULA*

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ABSTRACT: The mytilid *Botula* is shown to contain a single species, *B. fusca* Gmelin, which is widespread in tropical and sub-tropical waters of the Indian, Pacific and western Atlantic Oceans. Shell morphology and anatomy of this species are described. It is siphonate and bores in calcareous rocks and dead corals by means of non-acid secretions from large boring glands in the mantle folds anteriorly and posterodorsally. Its nearest living relatives are the species of *Lithophaga* s.s. and the genus is placed in the Lithophaginae along with *Adula*, *Lithophaga*, *Leiosolenus* and *Fungiacava*.

Recent classifications place the mytilid *Botula* Mörch 1853 in the Modiolinae (e.g. Soot-Ryen 1969, Keen 1971). Other genera placed in that group are non-siphonate byssally attached 'nestlers' while *Botula* is a siphonate, rock-borer. Lamy (1937) and other authors place *Botula* in the Lithophaginae. This paper reports results of an anatomical study of *Botula fusca*, undertaken to determine the affinity of the genus, to review its species taxonomy, and to determine the nature of the boring mechanism.

METHODS

Living specimens of *Botula fusca* were collected and studied at the Heron Island Marine Research Station, in the Great Barrier Reef Marine Park, Capricorn Zone. Supplementary preserved specimens were examined from several other Queensland and Western Australian localities. For comparative purposes sections were made of the pallial boring glands of *Leiosolenus lessepsianus*, also collected at Heron Island.

Isotonic $MgCl_2$ was used as an anaesthetic prior to dissection. Anatomical drawings were done from the anaesthetised specimens, free-hand or using a camera-lucida. Specimens for histological work were fixed in Bouin's solution, stored in 70% ethanol, routinely processed into paraffin blocks and sectioned at 5 μ . Sections were taken in a plane perpendicular to the mantle edge (transversely across the boring gland) and stained with Mayer's haematoxylin and eosin, Mallory's triple stain or Wiegert's iron haematoxylin. The periodic acid-Schiff reaction (P.A.S.) in conjunction with Alcian Blue (pH 2.35) was used as a test for acid or neutral mucopolysaccharides (Mowry 1956).

Shells of the specimens from which the anatomical study is based are deposited in the Museum of Victoria Melbourne, the Australian Museum Sydney, and the Western Australian Museum Perth. Abbreviations for repository institutions are as follows: AM—Australian Museum, Sydney. ANSP—Academy of Natural Sciences of Philadelphia, Philadelphia. BM(NH)—British Museum (Natural History), London. CAS—California Academy of Sciences, San Francisco. LACM—Los Angeles County Museum, Los Angeles. MCZ—Museum of Comparative Zoology, Harvard University, Boston. MNHN—National Museum of

Natural History, Paris. NMV—Museum of Victoria, Melbourne. SAM—South Australian Museum, Adelaide. SDNHM—San Diego Natural History Museum, San Diego. WAM—Western Australian Museum, Perth.

SYSTEMATICS

Class BIVALVIA

Family MYTILIDAE

Genus *Botula* Mörch 1853

1853 *Botula* Mörch, p. 55.

1939 *Botulopa* Iredale, p. 414. (Type species: *Botulopa silicula* *infra* Iredale, 1939 (= *M. fusca* herein))

TYPE SPECIES: *Mytilus fuscus* Gmelin 1791 by subsequent designation of Dall 1898.

DIAGNOSIS: Shell cylindrical, inflated, arcuate, smooth or finely concentrically striate, rather thin, white with a uniform thin, smooth, glistening brown periostracum. Umbos terminal, prosogyrate conspicuously incurved; hinge-line and ligament short, ligament opisthodontic, parivincular; margins smooth except for fine vertical striae beneath and immediately posterior to the ligament.

Incurrent and excurrent siphons long but usually divided; with a muscular septum within the tubular excurrent siphon and a prominent digitate ventral siphonal branchial membrane. Ctenidia filibranchiate and heterorhabdic, eleutherorhabdic. Boring glands present in the inner mantle folds anteriorly and posterodorsally. Posterior siphonal retractor muscles and scars present; anterior pedal retractors attach close to the margin of the hinge just below the umbos; posterior pedal-byssal retractors small.

Mussels which bore in dead corals, coral-rock or other calcareous rocks.

REMARKS: Mörch assigned to *Botula* only the species *arenaria* Meusch. (with *vagina* Lamarck, and *castaneus* 'Rumphius' Gray (*non* Say) listed as synonyms) and *fusca* Gmelin (with *Mytilus brunneus* Solander, *Modiola cinnamomea* Lamarck and *M. favanii* Potiez and Michaud listed as synonyms). Subsequently Dall (1898) selected *fusca* Gmelin as type. In these authors' opinion *arenaria*, a large, thin-shelled, siphonate mytilid which

burrows in soft substrates of the central Indo-Pacific region, is not congeneric with *fusca*, although its correct generic affinity is yet to be determined.

Botula most resembles *Lithophaga* s.s. in that the shell has a strong periostracum but no secondary, calcareous accretions, there are prominent plicate membranes in the roof of the mantle cavity, and boring is aided by chemical secretions from anterior and dorsal boring glands. It is easily distinguished from that genus by the short, arcuate shell form, the large, strongly incurved umbos, and the divided posterior siphons.

***Botula fusca* (Gmelin 1791)**

Figs 1 A-P, 2 B-F, 3-7

- 1785 *Mytilus cinnamominus* Chemnitz, pl. 82, fig. 731. (Refers to Lister, 1687, fig. 197.) (Type locality: Jamaica.) (Non-binomial publication.)
- 1791 *Mytilus fuscus* Gmelin, p. 3359. (Refers to Lister, 1687, fig. 197.) (Type locality: Jamaica.)
- 1793 *Mytilus cinnamomeus* Schreibers, p. 293. (Refers to Chemnitz, 1785, pl. 82, fig. 731.)
- 1807 *Modiolus cinnamomeus* Link, p. 147. (Refers to Chemnitz, 1785, pl. 82, fig. 731.)
- 1819 *Modiola cinnamomea* Lamarck, p. 114. (Type locality: l'Isle de France (Mauritius, Indian Ocean), leg. M. Desetangs.)
- 1819 *Modiola silicula* Lamarck, p. 114. (Type locality: 'Nouvelle Hollande' probably collected by Peron during the Baudin Expedition at Shark Bay, Western Australia.)
- 1844 *Modiolo favanni* Potiez & Michaud, p. 130, pl. 54, fig. 9. (Type locality: 'Exotique'.)
- 1892 *Lithodomus projectans* Tate, p. 130, pl. 1, fig. 1. (Type locality: 'Port Darwin'.)
- 1938 *Botula hawaiiensis* Dall, Bartsch & Rehder, 1938, p. 59, pl. 12, figs. 1-4. (Type locality: 'dredged by the U.S. Bureau of Fisheries Steamer "Albatross" at Station 3845 off the south coast of Molokai (Hawaii) in 60-64-0 fathoms on sand, pebble and shell bottom; bottom temperature 71°F'.)
- 1938 *Botula laysana* Dall, Bartsch & Rehder, 1938, p. 60, pl. 12, fig. 5. (Type locality: 'dredged by the U.S. Bureau of Fisheries Steamer "Albatross" at Station 3936, near Laysan Island (Hawaiian Islands) in 79-130-0 fathoms on small broken shell and coralline bottom; bottom temperature 68°F'.)
- 1939 *Botulopa silicula infra* Iredale, p. 415, pl. 6, fig. 26. (Type locality: Low Isles, Queensland.)
- 1959 *Botula cylista* Berry, p. 108. (Type locality: Punta Cameron, Mazatlan, Sinaloa, Mexico.)

See Table 1 for details of type specimens.

DISTRIBUTION: Widespread in the tropical and sub-tropical seas of the Indian, Pacific and western Atlantic Oceans. Apparently absent from the tropical eastern Atlantic. Figure 7 is based on verified museum specimen records and selected literature records.

HABITAT: *Botula fusca* is a boring mytilid inhabiting dead corals, coral rocks and other calcareous rocks. It is common in the intertidal zone and has been collected from suitable substrates to depths as great as 291-190 fathoms (off Hawaii, see Dall, Bartsch & Rehder 1938). It is often extraordinarily abundant in coral rocks and the coral-rock platform of the reef-crest zone, sometimes most commonly with the burrows opening on the underside of the rocks. The species may also be abundant burrowing in sloping beach-rock relatively high in the intertidal zone, e.g. along the southern shore of Heron Island (Queensland) below the research station. It is also known to burrow in the shells of other molluscs such as *Strombus gigas* (Chemnitz 1785) and oysters (Berry 1959). In northern Australia it is common boring in massed shells of rock-oysters (*Saccostrea*) high in the intertidal zone.

Gohar and Soliman (1963) have described and figured burrows of this species (identified as *Modiolus cinnamomeus* Bruguière) from the Red Sea. The burrow lacks a calcareous lining and is differentiated into two parts. The outer or siphonal part is roughly dumb-bell shaped in cross-section and it widens distally. The inner part, which is occupied by the shell, is kidney-shaped like the shell.

DESCRIPTION: Shell. White to pale brown, covered by a uniform tan to dark-brown or almost black glossy smooth periostracum. Cylindrical-arcuate, anterior and posterior ends broadly rounded; prosogyrate umbos large and terminal, sometimes conspicuously projecting and incurved. Ligament opisthodontic, parivincular, short and thick, resilium entire, sub-ligamental ridge lacking; hinge edentulous, margins smooth except for very fine, oblique striae on the dorsal margin beneath and immediately behind the ligament. Exterior smooth except for weak concentric growth striae and, in some cases, series of concentric ridges presumably representing successive growth phases (Fig. 1D, G; cf. *Lithophaga teres* and *L. antillarum*, Wilson 1979, p. 440, 448). Scars of anterior and posterior retractors weak but usually discernible, scar of siphonal retractor very weak but discernible.

Anatomy (see also Pelseneer 1911, Soot-Ryen 1955,

Fig. 1—A, B *Modiola cinnamomea* Lamarck; syntype (left valve of the whole specimen), MNHN (Paris); from 'l'Isle de France', leg. M. Desetangs. C, *Modiola silicula* Lamarck; type MNHN (Paris); from 'Nouvelle Hollande'. D, E, *Botula hawaiiensis* Dall, Bartsch & Rehder; holotype, USNM484180; off Molokai, Hawaii. F, *Botula laysana* Dall, Bartsch & Rehder; holotype, USNM335614. G, H, *Botula fusca* USNM257854; (34°05'N, 77°18'W). I, J, *Botula fusca* NMVF51471; Heron I., Queensland. K, *Botula fusca* USNM150313; St. George Cay, Belize. L, M, *Botula cylista* Berry; paratype; SDNHM428303; Punta Cameron, Mazatlan, Mexico. N, *Botula fusca* USNM173161; off Green Cay, Bahamas. O, P, *Botula silicula infra* Iredale; holotype, AMC60400; Low Isles, Queensland.

MYTILID BIVALVE *BOTULA*

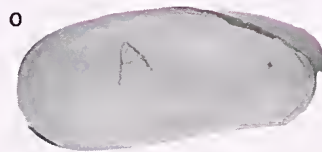
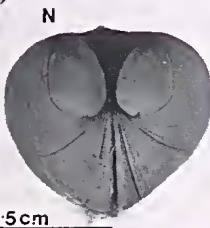
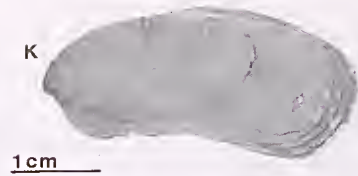
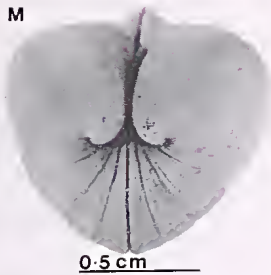
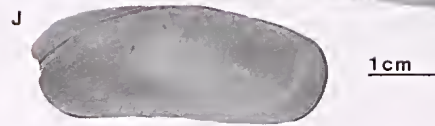
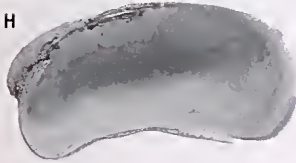
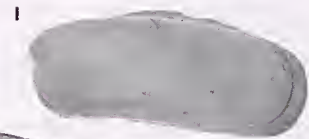
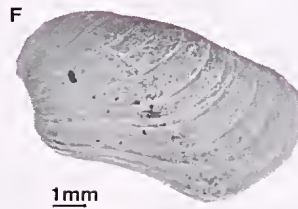
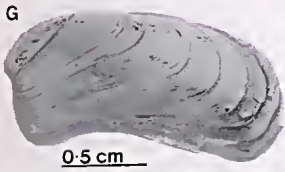
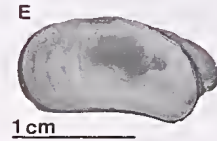
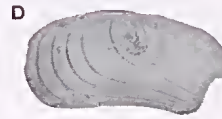
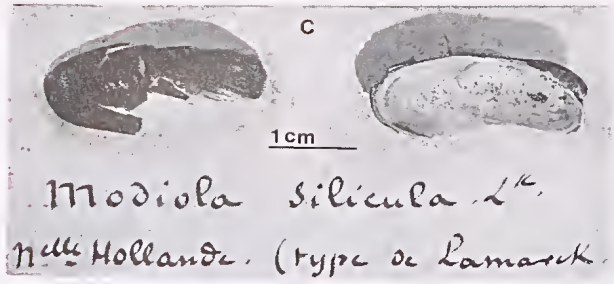
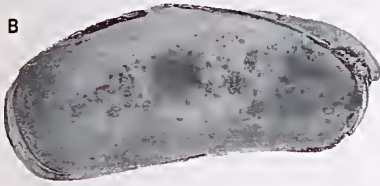
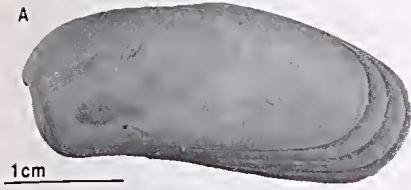


TABLE 1
LOCATION AND DIMENSIONS OF TYPES

		Length cm	Height cm	Width cm	Lig. Length cm
<i>Modiolus cinnamomea</i> Lamarck	2 syntypes: 1 whole shell and 1 left valve, Lamarck Collection, MNHN (Paris)	2.69 2.94	1.48 1.60	1.23 0.63(½)	1.26 1.54
<i>Modiolus silicula</i> Lamarck	Whole specimen, Lamarck Collection, MNHN (Paris)	2.47	1.12	1.06	1.37
<i>Modiolo Favanni</i> Potiez & Michaud	Type not located	—	—	—	—
<i>Lithodomus projectans</i> Tate	Whole specimen, SAMD14615	—	—	—	—
<i>Botula hawaiiensis</i> Dall, Bartsch & Rehder	Whole specimen, USNM484180	1.50	0.99	0.93	0.78
<i>Botula laysana</i> Dall, Bartsch & Rehder	Whole specimen, USNM335614	0.94	0.62	0.71	—
<i>Botulopa silicula infra</i> Iredale	Whole specimen, AMC60400	2.73	1.71	1.17	1.08
<i>Botula cylista</i> Berry	Holotype not located Paratype, whole specimen SDNHM42803	1.93	1.21	1.07	—

Gohar & Soliman 1963). Anterior adductor elongate-ovate and lies close to the antero-ventral margin. Posterior adductor ovate, rather small, conspicuously divided into 'quick' and 'catch' parts, and located quite far posteriorly. Anterior retractors moderately strong and insert close to the hinge margins below the umbones. Posterior retractors small (compared with byssal-attached mytilids such as *Modiolus*) insert above the antero-dorsal side of the posterior adductor; although separate pedal (anterior) and byssal (posterior) retractor strands arise contiguously (but distinguishable at the place of origin in the foot-byssus complex) they merge dorsally and insert as a single muscle block. A wide band of scattered siphonal retractor strands, originating from the mantle in the region of the siphon, inserts on the side of each valve antero-ventral to the posterior adductor.

The edges of the mantle from the umbo ventrally around to the postero-dorsal corner possess inner, middle and outer folds, as in other mytilids, the outer and middle folds adhering closely to the shell margins. The inner folds meet and fuse antero-ventrally from the umbo to a point a short distance behind the anterior adductor, and also along the postero-dorsal side; ventrally they are separate but appositioned in life to enclose the mantle cavity; posteriorly they are thickened, muscular and form extensible muscular siphons as in *Lithophaga*, *Leiosolenus* and *Adula* (see Pelseneer 1911, Yonge 1955, Soot-Ryen 1955, Fankboner 1971, Wilson 1979).

In most specimens the siphons are separate for most of their length (Figs 3, 6) but in odd individuals they are joined as in *Lithophaga* and *Leiosolenus*. They are fused by a horizontal branchial septum anteriorly, beneath which the gill axes attach.

The dorsal excurrent siphon is complete and tubular. Internally across its inner (anterior) end there is a thin but muscular suprabranchial valve or diaphragm with a

horizontal aperture and backward folded rim (Fig. 3). It forms a 'tube within a tube', presumably functioning as a velocity control device for the excurrent water flow. A similar structure occurs in *Lithophaga* and *Leiosolenus* (Wilson 1979).

The ventral incurrent siphon is flanked by muscular flaps which form a functional siphonal tube by apposition of the ventral edges. The branchial septum bears a ventral digitated 'valvular siphonal membrane' (Yonge 1955) like that of *Mytilus* (Kellogg 1915), *Lithophaga* (Yonge 1955, Wilson 1979), *Adula* (Fankboner 1971) and *Xenostrobus* (Wilson 1967). Soot-Ryen (1955, fig. 72) illustrates this structure. The membrane is usually asymmetrically digitated, with 10 or more digits on the large central flap, a smaller flap with 2 or more digits on each side, and a single digit in each lateral corner. Yonge (1955) suggested that this organ 'serves to shield the (outgoing) waste materials from the broad incoming stream of water'.

The ctenidia are filibranchiate, eleutherorhabdic and heterorhabdic. There are no inter-lamellar junctions as in *Mytilus*, but every 5th or 6th filament is a 'principal filament' (see Type B(1b) of Atkins 1937, text-fig. 4) with a connecting septum rising to about half way up the gill. The inner and outer demibranchs are about equal in height; ascending lamellae are a little shorter than the descending ones. The free edges of the ascending lamellae meet (but do not fuse with) the mantle or visceral mass. Conspicuous food grooves run along the bottom edge of each demibranch. The labial palps are broad and strongly plicate on their inner surfaces. The hind-gut is normally looped, has no special style-sac, and the rectum passes through the ventricle. The auricles are heavily pigmented reddish-brown. Pericardial glands are not evident on the walls of the pericardium. There is a dorsal cul-de-sac of the mantle cavity running forward

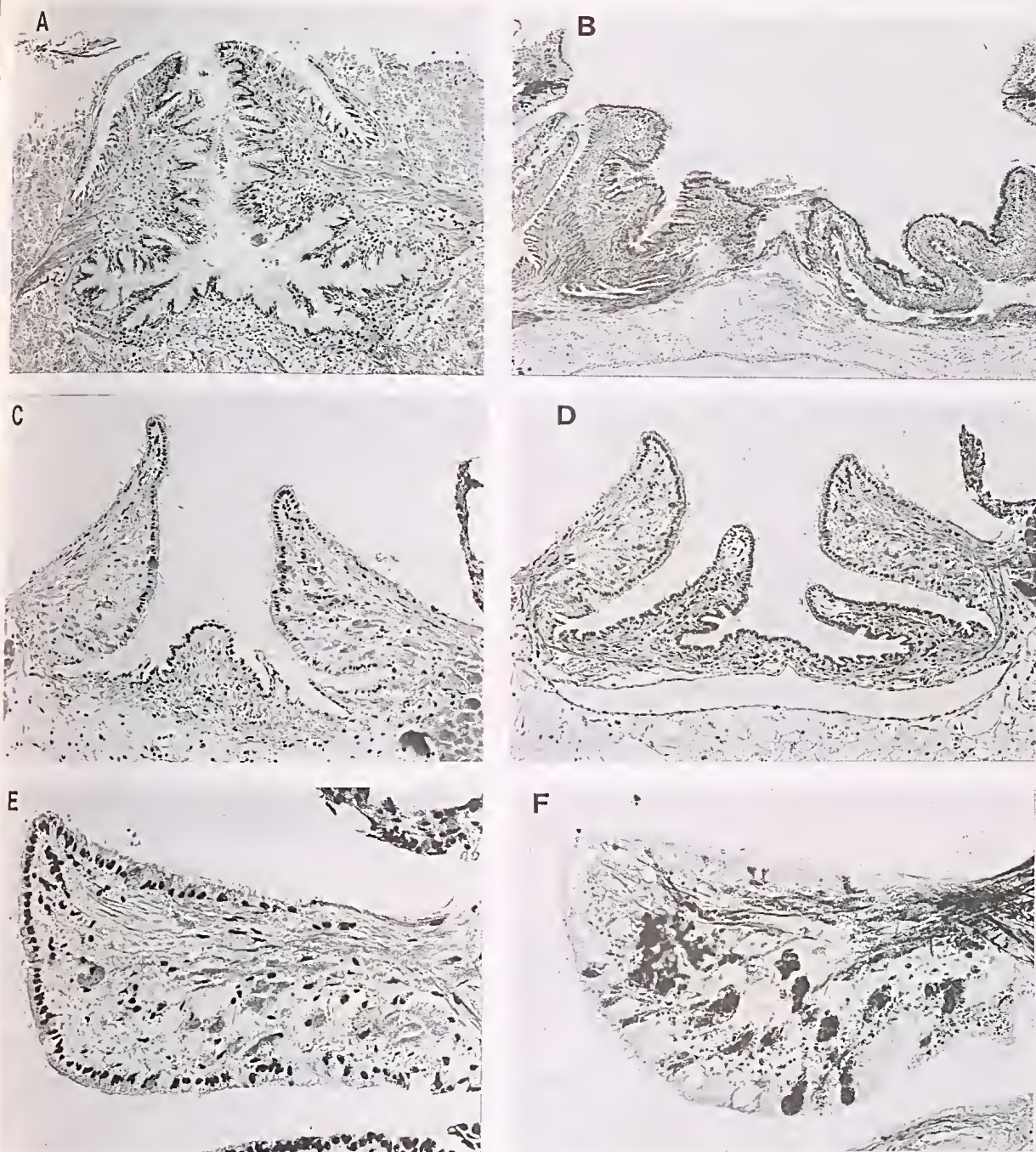


Fig. 2—Histology of the pallial boring glands in *Botula fusca* and *Leiosolenus lessepsianus* (the latter from a living *Acropora* colony) from Heron Reef, Queensland. A, *Leiosolenus lessepsianus* NMVF31815; horizontal section through the anterior gland showing a diverticulate lumen. Stained with H & E. $\times 160$. B, *Botula fusca* (NMVF31814); horizontal section through the anterior gland showing glandular middle and inner folds. Stained with H & E. $\times 87$. C, *Botula fusca* (NMVF31817); transverse section through the dorsal gland in an anterior position over the pericardium showing fusion of the inner folds down a mid-line ridge with small secondary lateral flaps, thick and glandular middle folds, and thin outer folds (visible on the right side only). Stained with H & E. $\times 260$. D, *Botula fusca* (NMVF31817); as for Figure C but sectioned further posteriorly, behind the pericardium and over the dorsal cul de sac of the mantle cavity; note the enlarged secondary flaps of the fused inner folds. Stained with H & E. $\times 220$. E, *Botula fusca* (NMVF31817); enlargement of the dorsal gland middle fold. Stained with H & E. $\times 530$. F, *Botula fusca* (NMVF31817); as for figure E, but stained with Mallory's Triple Stain. Note dark bodies stained red with Acid Fuchsin. $\times 530$.

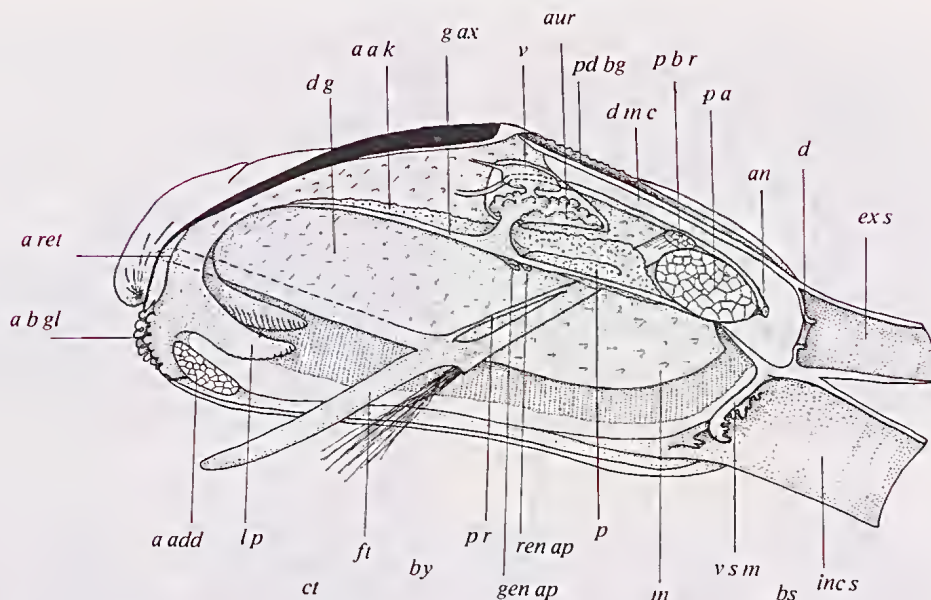


Fig. 3—Generalized diagram of the anatomy of *Botula fusca* from Heron Island, Queensland (NMVF51471). Left valve, mantle lobe and ctenidium removed; posterior siphons shown in sagittal section. Mid and fore-gut not shown. Abbreviations: *a b gl*—anterior boring gland. *a a k*—anterior arm of kidney. *a add*—anterior adductor muscle. *an*—anus. *a ret*—anterior retractor muscle. *aur*—auricle. *bs*—branchial septum. *by*—byssus. *ct*—ctenidium. *d*—diaphragm within excurrent siphon. *dg*—digestive gland. *d m c*—dorsal mantle cavity cul de sac. *ex s*—excurrent siphon. *ft*—foot. *g ax*—gill axis (left side, gill detached). *gen ap*—genital aperture. *int*—intestine. *inc s*—incurrent siphon. *lp*—labial palps (left). *m*—mesosoma *m & o m f*—middle and outer mantle folds. *pa*—posterior adductor muscle. *pa k*—posterior arm (dorsal and ventral loops) of kidney. *pd b gl*—postero-dorsal boring gland. *p b r*—posterior byssal retractor muscle. *pl m*—plicate membranes. *pr*—posterior pedal retractor muscle. *rec*—rectum. *ren ap*—renal aperture. *s r m*—siphonal retractor muscles. *v*—ventricle. *v s m*—valvular siphonal membrane.

above the posterior adductor and rectum to the posterior wall of the pericardium as in *Mytilus*, *Lithophaga* and *Modiolus*. Left and right kidneys comprise a relatively thick-walled tubular organ, lined with heavily pigmented (reddish-brown) tissue, with renopericardial openings in the anterolateral corners of the pericardium. An arm of the kidney tube runs forward for a short distance above the ctenidial axis; the broader part of the kidney runs backwards to the anterior and ventral edges of the posterior adductor and then recurves ventrally, lying above the gill axis, terminating at the renal aperture in the roof of the mantle cavity in a position approximately below the centre of the pericardium. There are large, conspicuous plicate membranes on both sides and the full length of the gill axes (Fig. 4).

Gonad tubules lie superficially over the digestive gland dorsally, fill much of the space between the diverging posterior retractors, invest the mantle lobes, and fill a large mesosoma. The genital aperture is located on a papillum adjacent to but not contiguous with the renal aperture (Fig. 4).

Boring glands are located in the middle and inner folds of the mantle lobes anteriorly and in the middle folds posterodorsally. The anterior boring gland is a conspicuous, convoluted organ located between the anterior adductor and the umbos, just below the junction of the outer mantle folds (Fig. 3). Middle and inner mantle folds (Fig. 2B) are covered with ciliated columnar epithelium composed of cells 9–24 μ in height. The middle fold has a longitudinal furrow on its median surface, also lined with ciliated cells. A shallow layer of heavily vacuolated subepithelial cells overlies a dense bundle of collagen fibres which runs longitudinally along the edge of the fold. This bundle occupies the bulk of the middle mantle fold so that secretory activity is restricted to the peripheral area. The inner mantle folds are convoluted and covered with a minutely folded epithelium of secretory and ciliated cells 16–22 μ in height. The subepithelial region is a loose matrix of collagenous fibres with a large number of spaces. The glands are drained by a large number of short, branched ducts, all lined with ciliated columnar epithelium. In the

epithelium, and some vacuoles in the subepithelium, bodies 7-15 μ in diameter can be seen. Presumably, these are secretory droplets; they show a positive P.A.S. reaction, but do not stain with Alcian Blue.

In the posterodorsal region behind the ligament the inner mantle lobes appear to have little secretory activity. The epithelial cells are cuboidal with round nuclei and have no visible inclusions. However, the middle mantle folds in this region are glandular (Fig. 2 C-F) with many eosinophilic inclusions staining red with Acid Fuchsin (Fig. 2F), and a secretory, ciliated epithelium of columnar cells 10-12 μ in height. The subepithelium is a loose matrix with a large number of intra and extra-cellular droplets which can be seen to pass to the exterior through minute and otherwise invisible ducts. These secretory droplets stain strongly P.A.S. positive using an Alcian Blue, P.A.S. technique.

Ventrally, the middle folds of the mantle lobes do contain secretory cells, but there is no enlarged gland. Nor was any glandular structure observed in the posterior siphons.

DISCUSSION

MORPHOLOGICAL VARIATION AND TAXONOMY OF THE SPECIES

Intra-population variation in shell morphology of these mussels is extreme, apparently relating to the nature of substrates in which they bore. No geographic patterns of variation could be discerned, even between the Western Atlantic and Indo-West Pacific populations. The few specimens we have seen from the eastern Pacific fall well within the range of variation of the entire series. We can find no morphological grounds for giving that population separate taxonomic status and we confidently place *Botula cylista* Berry in the synonymy of *B. fusca*.

One feature of interest is the colour of the periostracum. In some specimens it is light chestnut brown; in others, it is dark brown or black. Both colour forms are found throughout the species' range, and in some places (e.g. Heron Island) they may be found burrowing in the same rocks. The significance of this dimorphism is unknown to us.

Anatomically, this mussel is quite uniform. The only character showing variation is the digitation on the valvular siphonal membrane on the ventral side of the branchial septum (see anatomical description and Fig. 5A, B). However, there is no evidence of geographic pattern in this variation.

We have pondered at length the widespread nature of this mussel and whether more than one species might be involved. The logical *modus operandi* must be to assume a single species unless, or until, there is evidence of reproductive isolation or morphological or other evidence which implies genetic divergence. In this case (with the worrying exception of periostracum colour) evidence of discrete morphs is lacking. Therefore we conclude that there is but a single living species of *Botula*, widely distributed in coastal tropical waters with the apparent exception of the eastern Atlantic.

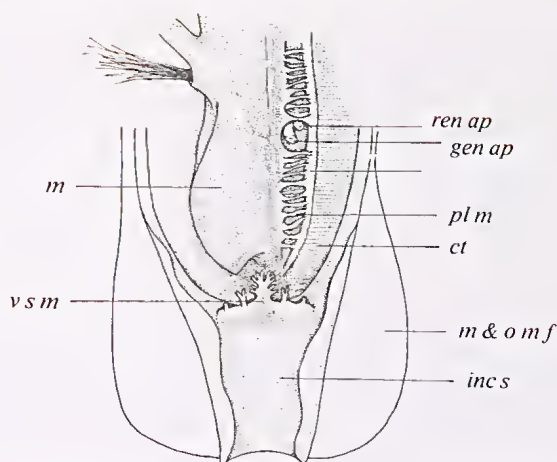


Fig. 4—Diagram of posteroventral area; mesosoma displaced to the right exposing the plicate organs, genital aperture and renal aperture of the left side between the visceral mass and the gill axis. (Specimen from Heron I., Queensland; NMVF51471).

FOSSIL RECORD

Botula fusca appears to have a long fossil history as well as a wide distribution. Dall (1898) reported a fossil under this name from the Oligocene of Florida. *Botula cordata* (Lamarck 1807) from the Eocene of France, Senegal, Libya and Egypt (see Freneix & Gorodiski 1963) and *Lithophaga mcknighti* Hanna 1927 from the Eocene of California (see Moore 1983, pl. 19, figs 9, 10) may also be this species. A plastotype of the latter fossil in the collections of the CAS is indistinguishable from living *B. fusca* shells.

SPECIES NOMENCLATURE

The first published reference to this species is a poor but recognizable illustration by Lister (1687). No locality is given specifically for this figure but it is framed with a figure of a *Modiolus* which bears the word 'Jamaic'.

Chemnitz (1785) published a reasonably good figure, referred to duplicate material in the Spengler collection from the Nicobar Islands, and stated that the species bores in the shells of other molluscs and corals and that his own material was found in a West Indian specimen of *Strombus gigas*. With this illustration, Chemnitz introduced the name '*Mytilus cinnamominus*'. It is clear that the Lister and Chemnitz figures illustrate the same species.

In the *Portland Catalogue*, Lightfoot (1786, p. 104, number 2275) listed *Mytilus Brunneus* but gave no reference or description. Although some authors (e.g. Lamy, 1937, p. 179) place this name in the synonymy of *cinnamomea* (= *fusca*) it should be regarded as a *nomen nudum*.

In 1791 Gmelin referred to the figure by Lister and provided for it the name '*Mytilus fusca*' but gave no locality data. Subsequently, Schreibers (1793) and Link



Fig. 5—Valvular siphonal membrane of *Botula fusca* (compare also with Fig. 2): A, ex Brittomart Reef, Queensland (NMVF51472). B, ex Isla Tortuga, Venezuela (redrawn from Soot-Ryen 1955, text-fig. 72).

(1807) used the name '*cinnamomeus*' citing the Chemnitz illustration.

In 1819 Lamarck used '*Modiola cinnamomea*' citing both the Chemnitz and the Lister figures (referring to the latter as 'var. (b)') but also referring to specimens in his own collection from 'l'Isle de France'. Types exist in the MNHN (Paris) Lamarck Collection (Fig. 1A, B). There are two samples. One sample consists of a whole specimen and a single left valve, labelled as the l'Isle de France material collected by M. Desetangs; the specimens have a chestnut brown periostracum. The other sample consists of four whole specimens and two valves without locality and the type status of this material is uncertain.

In the same publication Lamarck described another mussel, under the name *Modiola silicula*, from New Holland (Western Australia). The type (Fig. 1C) is a whole specimen in the MNHN (Paris) Lamarck Collection. It is clearly conspecific with the types of *M. cinnamomea* Lamarck, although it possesses a dark brown periostracum.

The publication of Chemnitz is not an accepted source of available names and so *M. fusca* Gmelin 1791 becomes the first available name which is based on the Lister figure and we may assume that the type locality is Jamaica in the Atlantic.

The names *M. cinnamomea* Lamarck and *M. silicula* must be associated with the Indo-West Pacific population because of the clearly designated Indian Ocean localities with the type material. Some authors (e.g. Iredale 1939) have assumed that the Atlantic and Indo-West Pacific populations are different species. In that case *M. fusca* Gmelin would be the available name for the Atlantic form, but *M. cinnamomea* Lamarck could not be used for the Indo-West Pacific form because the name was already validly used by Schreibers and Link for the Chemnitz figure (i.e. it is a subjective synonym of *M. fusca* Gmelin). It was for this reason that Iredale used the second available name of Lamarck, i.e. *silicula*, for the Indo-West Pacific population when he unnecessarily provided the subspecific name *infra* for the Queensland form (Fig. 1O, P). However, this problem

becomes unimportant once it is accepted that there is but a single species widely distributed in the Indian, Pacific and Atlantic Oceans. The oldest available name, *M. fusca* Gmelin, must be used for all. It is unfortunate that this name is based on a poor illustration, with dubious provenance, in a rare publication, and that there is no type.

BORING MECHANISM

Boring in calcareous substrates is achieved by certain mytilids by mechanical abrasion (rubbing of the shell valves against the burrow wall), by chemical means, or by a combination of the two. Boring glands in the mantle folds have been described in species of *Lithophaga* (Pelseneer 1911, Turner & Boss 1962, Wilson 1979, Morton & Scott 1980) *Leiosolenus* (Yonge 1955, Wilson 1979, Kleeman 1980, Morton & Scott 1980) and *Fungiacava* (Goreau, Goreau, Soot-Ryen & Yonge 1969, Goreau, Goreau & Yonge 1972).

Morton and Scott (1980) have described the histology and morphology of anterior and posterodorsal boring glands in the middle mantle folds of a number of *Lithophaga* and *Leiosolenus* species. They established that there is a 'progressive degree of complexity from simple epithelial to ducted sub-epithelial structures coinciding with increasing specialization of habitat from natural limestone to species specific live coral dwellers.' They also described a siphonal gland in the more specialized species (of *Leiosolenus*).

Lithophaga lithophaga (Linnaeus) and *L. teres* (Philippi) which bore in limestones and dead corals, are examples of species with large but histologically simple anterior and posterodorsal boring glands and no siphonal glands. *Leiosolenus simplex* (Iredale) (= *lessepsiana*, see Wilson 1979) and *Leiosolenus mucronata* (Philippi) are the extreme examples of the specialized live-coral dwellers.

In *Fungiacava eilatensis*, which bores in living *Fungia*, boring is exclusively chemical. The shell never comes in contact with the walls of the burrow and there are large boring glands in the middle mantle folds, including in the siphonal regions (Goreau *et al.* 1972).

Yonge (1955) compared the boring mechanisms of '*Botula*' and '*Lithophaga*', concluding that they are essentially mechanical in the former and chemical in the latter. Although the results of that study are not disputed here, they apply not to *Botula* and *Lithophaga* but to *Adula* and *Leiosolenus*. The species studied were *Adula falcata* (identified as *Botula (Adula) falcata*) and *Leiosolenus plumula* (identified as *Lithophaga plumula*).

Gohar & Soliman (1963) discussed the boring mechanism of *Botula fusca* (misidentified as *Modiolus cinnamomeus*) from the Red Sea, but failed to observe boring glands. They described the boring mechanism in this species as 'by mechanical abrasion, in a rocking movement'.

In this study it is shown that *Botula fusca* has large but histologically simple anterior and posterodorsal boring glands and lacks siphonal glands, thus matching the

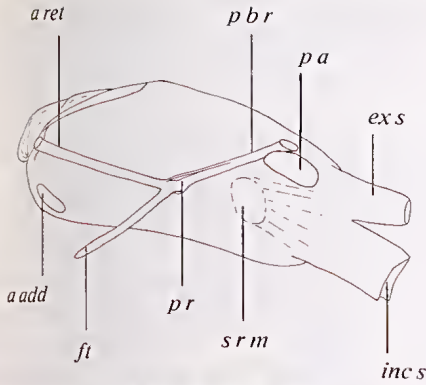


Fig. 6—Musculature of *Botula fusca*. (Specimen ex Heron I., Queensland; NMVF51471).

condition of *Lithophaga* s.s. and the least specialized *Leiosolenus* species which bore in calcareous rocks and dead corals.

Morton & Scott (1980) postulate a 'progressive reduction in shell length relative to width and height' and 'a progressive reduction in size of the adductor and byssal retractor muscles' in the *Lithophaga-Leiosolenus* series correlating with habitat specialization. *Botula fusca* is short, cylindrical, blunt ended and has very small posterior byssal retractor muscles, and it does not fit this postulated morphological trend.

Many authors (Carazzi 1903, Pelseneer 1911, Yonge 1955, Franc 1960, Turner & Boss 1962) have supposed that the chemical agent secreted by the boring glands of lithophagines is a free acid and the organs are referred to in the older literature as the 'acid glands'. More recent authors accept a contrary view that the boring agent is a calcium-binding neutral mucoprotein, following the results of histo-chemical studies on *L. lithophaga* by Jaccarini *et al.* (1968). In that species secretory cells from the boring glands are strongly P.A.S. positive and do not stain with Alcian Blue, thereby excluding the possibility of an acid mucopolysaccharide secretion. The results of our histo-chemical tests confirm that this is the case in *Botula fusca* also.

FAMILY PLACEMENT OF *BOTULA*

Although Lamy (1937) placed *Botula* with *Lithophaga*, Dall (1898) Ircdale (1939) Keen (1937, 1971) Soot-Ryen (1955, 1969) and others have considered that *Botula* is a relative of *Modiolus* in view of similarity of shell form though noting the peculiar musculature of *Botula*. In fact, the cylindrical, slightly arcuate shell of *Botula* with its large, terminal and incurved umbos and wide, blunt anterior end, is quite atypical of *Modiolus*. Nor does *Botula* possess a hirsute periostracum which is an important feature of *Modiolus*; the periostracum is thin and glossy smooth.

Anatomically there are many differences besides musculature. Most significantly, *Botula fusca* has large extensible siphons with an internal diaphragm within the excurrent siphon, boring glands in the mantle folds and a large, digitate valvular siphonal membrane on the ventral side of the branchial septum and the posterior retractor muscles are small. These major anatomical characters exclude any possibility of a close affinity with *Modiolus*. On the contrary, these features and the burrowing lifestyle are consistent with a lithophagine affinity.

Wilson (1979) commented on significant anatomical differences between *Lithophaga* s.s. (as represented by *L. lithophaga* Linnaeus, *L. niger* d'Orbigny, *L. teres* Philippi, and *L. antillarum* d'Orbigny) and the series of species which possess secondary calcareous accretions on the posterodorsal parts of the valves. Further evidence for generic separation of these two groups of boring mussels has been provided by Morton and Scott (1980) who showed differences in the structure and location of the boring glands.

Waller (1983) has shown that the periostracum of the *Lithophaga* s.s. series has a mineralized outer layer containing calcium hydroxyl-apatite, with an X-ray diffraction pattern like that of dahllite, apparently a device for hardening the periostracum helping to protect the shell from abrasion during burrowing. This substance is lacking in the periostracum of the species with secondary calcareous accretions which appear to be an alternative

TABLE 2
DIAGNOSTIC CHARACTERS OF THE GENERA OF LITHOPHAGINAE

ADULA	LITHOPHAGA	BOTULA	LEIOSOLENUS	FUNGIACAVAL
Shell elongate—cylindrical	Shell elongate—cylindrical	Shell short—cylindrical	Shell elongate—cylindrical	Shell high, ovate
Umbones subterminal	Umbones subterminal	Umbones terminal, strongly incurved	Umbones subterminal	Umbones subterminal, strongly incurved
Boring glands lacking	Anterior and posterodorsal boring glands present, simple; siphonal boring glands lacking.	Anterior and posterodorsal boring glands present, simple; siphonal boring glands lacking.	Anterior and posterodorsal glands present, simple or complex; siphonal boring glands present.	Boring glands present.
?	Plicate membranes present.	Plicate membranes present.	Plicate membranes lacking.	?
Siphons undivided	Siphons undivided	Siphons divided	Siphons undivided	Siphons undivided

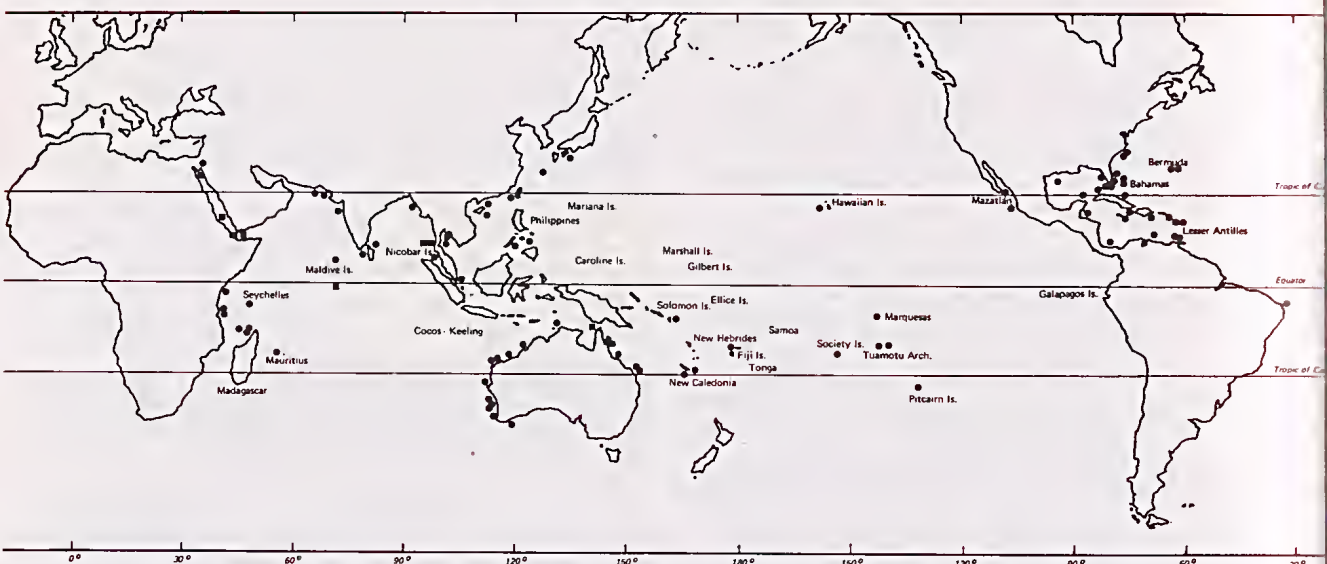


Fig. 7—Distribution of *Botula fusca* based on specimens in museum collections examined by the authors (●), and selected literature records (■).

device serving, in part, the same function. For these reasons *Leiosolenus* is here restored to generic rank to include the species which possess secondary calcareous accretions on the shell valves but lack a mineralized outer layer in the periostracum, and possess pocket-like supra-branchial chambers between the gill axes and the visceral mass but lack plicate membranes.

Goreau *et al.* (1970) argued that *Fungiacava* is most closely related to *Solamen* and *Crenella* (subfamily Crenellinae) but Morton & Scott (1980) favour a lithophagine affinity for this unusual genus. The latter view is accepted here.

It is proposed here that the subfamily Lithophaginae be redefined to include five genera of siphonate, rock-boring mytilids (Table 2): *Adula* which bores by mechanical means and *Lithophaga*, *Leiosolenus*, *Fungiacava* and *Botula* which bore by means of chemical secretions from boring glands located in the mantle folds. *Botula* appears to be most closely related to *Lithophaga*.

LOCALITY RECORDS

The following list is based on verified museum specimen records and selected literature records where these add significant information. Abbreviations and spelling are as given on the original record.

ATLANTIC

North Carolina: In coral rock, 14 fms, 34°05'N, 77°18'W (USNM); 14 fms, 25 miles SE of Cape Fear (USNM); 18 fms, 27 miles SE of Cape Fear (USNM).

South Carolina: Sullivan I. (MCZ).

Florida: Miami (ANSP, MCZ, USNM, BMNH); 3-30 fms off Miami (USNM); 25-60 fms, off Fowey Light (USNM); 30 ft, 8-10 m. W of Mullet Key, Fort Dade (ANSP); 10-14 fms, off Palm Beach (ANSP); Middle Grounds, NW of Johns Pass, off St. Petersburg (MCZ); Tampa Bay (MCZ); 65 fms off Western Dry Docks (USNM); Key West (MCZ, ANSP, USNM); 65 fms off Ragged Key (USNM); 1 m off Soldier Key (MCZ); Bonefish Key (ANSP); in soft rock, No Name Key, near Big Pine Key (USNM); 15-16 fms, Tortugas (USNM); Garden Key (CAS).

Texas: 103 and 107 mi. SE of Galveston (MCZ).

Bahamas: Off Green Cay (USNM); Grand Bahamas (USNM); N end Elbow (Little Guana) Cay, Great Abaco (ANSP); Bimini Lagoon (ANSP); 3 fms, Caicos Bank off Ambergris Cay (MCZ); Andros (MCZ).

Bermuda: (BMNH); 80-100 fms, ¼ mi. S of Castle Road (MCZ); 4-5 fms, Castle Roads, Castle Harbour (MCZ).

Cuba: 25 fms Cabanas Harbour (USNM); Cape Cajon (USNM); 1-12 fms Bahia Honda (USNM); Cao Cruz del Padre, Santa Clara (USNM).

Dominican Republic: Santa Barbara da Samang, Santo Domingo (MCZ).

Haiti: (BMNH).

Puerto Rico: Punta Arenas, Vieques (USNM); Mayaguez Harbour (USNM).

Virgin Islands: St. Thomas (ANSP, MCZ, USNM).

Barbados: 10-20 ft, off Pelican I. (USNM).

Belize: Coral reef near St. George Cay (USNM).

Trinidad: Chaguaramas Bay (USNM).

Tobago: E of Pigeon Point (USNM).

West Grenada: 6 ft, Morne Rouge Bay (ANSP); 30 ft, ½ m W of Fort George, St. George (ANSP).

St. Lucia: Boat Harbour, Castries (MCZ); Marigot Harbour (MCZ).

Jamaica: (Type locality): Lister (1687); (MCZ).

Mexico: 25 fms, off Cape Catoche, Yucatan (USNM).

Curacao: 30 ft, Oranjestad Lagoon, Aruba I. (ANSP).

Panama: 10 fms Limon Bay (CAS). 10 fms, 2 m. off Colon (MCZ).

British Honduras: Punta Gorda (ANSP); 12 ft, reef E of Cangreja Cay (ANSP).

Venezuela: Isla Tortuga (Soot-Ryen 1955).

Brazil: 20 fms, off Cuba Sao Roque 6°59'S, 34°47'W (USNM).

EASTERN PACIFIC

Mexico: Boring in *Ostrea iridescens*, Punta Camaron, Mazatlán (SDNHM). Mazatlán (CAS); 5-10 fms, Maria Madre Is., Tres Marias Group (CAS).

INDO-WEST PACIFIC

Madagascar: 0-5 ft, E of Nosy Ambariole, SE of Nossi Bé (ANSP); 16 fms, 2-3 mi S of Nosy Iranja, 32 mi. SW of Nossi Bé (ANSP); 0.6 ft, E Bay between Nosy Ambariole & Nosy Ambariotelo, SE of Nossi Bé (ANSP); 0.8 ft, Pointe Lokobe, SE Nossi Bé (ANSP); 0.6 ft, Iles Radama, 52 mi S of Nossi Bé (ANSP).

Kenya: Shimoni (BMNH).

Mauritius: MNHN (Paris); (BMNH); 0.8 ft, Pointe Fayette (ANSP); Blue Bay (ANSP).

Aldabra: (BMNH).

Seychelles: (BMNH); 30-36 ft, Cerf I., NE Mahé (ANSP); 18 ft, St. Anne I., NE Mahé (ANSP).

Zanzibar: (BMNH); 11-12 fms, Pwakuu I. (ANSP); 11 fms, 1 mi W. Nyange I. (ANSP); 5-8 fms, 3 mi. SE Bawi I. (ANSP); 0-6 ft, Chumbe I. (ANSP).

Red Sea: Eilat (WAM); Djibouti and Aden (Lamy, 1937); Ghardaga (Gohar & Soliman 1963).

Aden: (BMNH).

Iran: Gadani, E of Samniani, Baluchistan (BMNH).

Pakistan: Ibrahim Maidari, near Karachi (BMNH); Karachi (CAS).

India: Hare I., 6 mi SW Mandapam, Gulf of Mannar (ANSP); Bombay (MCZ, BMNH).

Sri Lanka: Pearl Banks, Gulf of Mannar (BMNH).

Burma: Arakan and Mergui (BMNH).

Thailand: Kata, near Khao Lan, Phuket I. (ANSP); Mutapone I., Chumpon (MCZ); 1-30 fathoms in old coral blocks, Cape Liant to Koh Chang (Lyngé 1909).

Nicobar Islands: (Lyngé 1909).

Mergui Archipelago: (Lyngé 1909).

Maldivé Archipelago: Addu Atoll (BMNH); Suvadiva Atoll (Lyngé, 1909).

Malaysia: Palau Bidang, N of Penang (BMNH).

Singapore: Boring in coral rocks, Palau Salu (WAM).

Philippines: Boring in dead coral, Apat Bay, Calauage Bay, S. Quezon (WAM); 15 fms, N of Laminusa Is., Siasi, Sulu (WAM); 1 fm, dead coral, Laguio Pt., Lopez Bay, S. Quezon (WAM).

Taiwan: (Wen-Lung Wu, 1980).

Okinawa: Ryuku Is. (ANSP).

Japan: Shigeo Hashimoto, Kii (ANSP).

People's Republic of China: Coast of Guandong to Hainan I. (Tsi & Ma, 1980).

Solomon Islands: 180 ft. boring in dead coral boulders, W side of Malapaina I., SE San Cristobal (WAM).

New Caledonia: 0-10 ft, Baie de l'Orphelinat, Noumea (ANSP); Recaudy Reef, Noumea (ANSP); 50 ft, 3 mi NE Dunebea Pass (ANSP); 0-18 ft, Santa Marie (Isle Ngea), Magenta (ANSP).

Fiji: (ANSP, MCZ, CAS).

Society Islands: Fauni Pt., Bora Bora (USNM).

Tuomotu Archipelago: 10 fms, coral rocks, Rangiroa Lagoon (WAM); Ngarumaoa Is., Raroia (USNM); Tatau I. (USNM).

Marquesas: 37-40 fms, W of Fatu Hiva (USNM).

Pitcairn I.: 40-58 fms (USNM).

Australia: Northern Territory: Darwin (Tate 1892).

Queensland: Torres Strait (Melville & Standen, 1899); 3 m, in dead *Porites*, Watson Bay, Lizard I. (WAM); in dead coral, Rocky Point, Lizard I. (WAM); reef flat, Low Isles (WAM, AM); Britomart Reef (NMV); South Keppel I. (WAM); in dead coral, outer reef rim and reef crest, Heron I. (WAM); 4 m, reef-front slope, in dead coral, Heron I. (WAM); boring in beach-rock, south side of Heron I. (NMV). *Western Australia* (All WAM): Upper intertidal zone, boring in oyster shells, Derby; 22 fms, 40 mi. W of Cape Jaubert; oyster shells, upper intertidal zone, Kendrew I., Dampier Arch; dead coral rocks, reef ridge, Kendrew I., Dampier Arch; 3 m, Rosemary I., Dampier Arch; 10 mi, S of Exmouth, Exmouth Gulf; 18 m, shell, coral rubble & lithothamnion nodules, 5 km ESE of Cape Heirisson, Shark Bay; reef flat, Long I. Passage, Abrolhos; 15 m, 24 km N of Dongara; 82.3 m, 35 km W of Jurien Bay; Mosman Beach & Hall Bank, Fremantle; 11-17 m, off Fremantle; 10 fms, 1½ m W of south end of Garden I.; 54 ft, Dunsborough, Geographe Bay; 46 m, in dead coral, Cheyne Beach.

ACKNOWLEDGEMENTS

We acknowledge with thanks financial support from the National Museum of Victoria Council for field work and technical assistance, and facilities provided by the California Academy of Sciences during the drafting of the manuscript. Financial support for travel to European and American museums was generously provided by the Ian Potter Foundation of Melbourne. We are particularly grateful to Professor J. V. Hurley and Mr. Dennis Cahill of the Department of Pathology, Univer-

sity of Melbourne, who gave kind permission to use the facilities of their department. The staff of the Central Laboratory, Department of Pathology also provided valuable advice on histological work. Mr. Jack Smith, Department of Pathology took the photomicrographs and Mr. Frank Coffa of the National Museum of Victoria photographed the shell specimens. Thanks are also due to staff of many museums who spent much time preparing loans of specimens in their custody. Dr. Michael Ghiselin and Dr. Vida Carmen Kenk kindly read and criticized the early drafts of the manuscript.

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REVIEW OF TAXONOMIC POSITION OF AUSTRALIAN AND NEW GUINEAN SPECIES PREVIOUSLY ASCRIBED TO *MACRONEMA* (TRICHOPTERA: HYDROPSYCHIDAE)

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ABSTRACT: The taxonomic position of Australian and New Guinean species previously referred to the genus *Macronema* s.l. is reviewed and generic changes implemented. A new genus, *Baliomorpha*, is established for 4 Australian species (*banksi* (Mosely), *dubia* (Ulmer), *pulchripenne* (Tillyard), *urbana* sp. nov.) and 5 species (*loriai* (Navás), *caudicea* sp. nov., *chiloma* sp. nov., *echinata* sp. nov., *pezidion* sp. nov.) from New Guinea. Three closely related species (*saundersi* (McLachlan), *loriai* (Navás), *auriferum* sp. nov.) all from New Guinea, are placed in the genus *Macrostemum*; of these, *saundersi* is known also from Cape York Peninsula. The position of 2 other New Guinean species (*wallacei* McLachlan, *dulce* McLachlan) is unresolved.

Seven species names have been applied to the genus *Macronema* Pictet s.l. in Australia. Only 3 of these are now recognised as valid; and a fourth species, *saundersi* (McLachlan), previously known from New Guinea, is now recorded from northeastern Australia. Of these four species, 3 are placed in a new genus, *Baliomorpha*, together with a new Australian species (*urbana* sp. nov.), while the fourth, *saundersi*, is referred to *Macrostemum* Kolcnati, as proposed by Flint and Bueno-Soria (1982).

Both genera are represented in New Guinea. Australian species are restricted to a narrow eastern belt more or less corresponding to the Great Dividing Range, from Cape York Peninsula to Victoria. None has been recorded from Tasmania.

McLachlan (1862) recognised *Monopseudopsis inscriptus* Walker 1852 as a species of *Macronema*, and noted that the species name had already been used in the genus. He renamed it *Macronema australe* McLachlan. No further *M. australe* specimens have been recognised in subsequent studies, including the present in which extensive material was examined. This raised doubts about its identity and country of origin. A general literature check indicated close similarities in the wing pattern of the type of *australe* with that of the common North American species *Macrostemum zebratum* Hagen (Fig. 45). Dr Barnard of British Museum (Natural History), London, confirmed that "the wing pattern and genitalia of type (*australe*) both agree entirely with specimens of *zebratum* in our (BMNH) collection, and the label 'New Holland' must therefore be wrong" (Barnard in litt. 1983).

Wrong locality labels on specimens originating from the 'Entomological Club' and described by Walker have been recorded before—e.g. the type of *Notidobia* (= *Anisocentropus*) *latifascia* Walker bears the locality label 'North America', but was later found to be an Australian species.

As the name *inscriptus* Walker 1852 was unavailable because of homonymy, and *zebratum* Hagen 1861 predates *australe* McLachlan 1862, the latter is suppressed to synonymy and removed from the list of Australian species.

Two other species names are also suppressed: *tristis* Banks 1939 preoccupied by *triste* Navás 1916 has been replaced by *banksi* Mosely 1953, and *torrenticola* Korb 1964 is a new synonym of *banksi* Mosely 1953.

The general statement by Flint and Bueno-Soria (1982) that all Australian species listed in the Fischer Catalogue (1963, 1972) should be transferred to the genus *Macrostemum* is unacceptable and requires some amendments.

The Australian-New Guinea species complex belongs to two quite distinct groups (Tables 1 & 2), neither of which is accommodated entirely satisfactorily by the diagnoses of *Macronema* or *Macrostemum*. One of the groups is considered generically distinct as *Baliomorpha* which includes 4 Australian and 5 New Guinean species. The second group is retained in *Macrostemum*.

The Australian-New Guinean group of species now placed in *Macrostemum* differs in a number of features from the typical North American representatives. If these differences are shared by further species in the SE Asian-Sunda Archipelago area, it might be necessary to unite them into a separate genus. This is outside the scope of this paper. Two species, *dulce* McLachlan from Misool Island and *wallacei* McLachlan from New Guinea, unfortunately were not available for this study and their identity at this stage remains uncertain.

Dcan (1984) reports that larval features of some Australian species, here referred to *Baliomorpha*, differ from both *Macronema* and *Macrostemum*.

The figures of the wing venation have been prepared with the aid of a camera lucida, where possible from detached wings, relaxed, denuded of hair and temporarily mounted on glass slides. Figures of genitalia were prepared from abdomens macerated and cleared in potassium hydroxide, then washed and transferred to glycerine for drawing and permanent storage. Dissected and figured specimens are identified by the author's notebook number with the prefix 'PT-'.

The following abbreviations are used for depository institutions: ANIC, Australian National Insect Collection, Canberra; BMNH, British Museum (Natural History), London; BPBM, Bernice P. Bishop Museum, Honolulu; MCG, Museo Civico di Storia Naturale,

Genova; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; MNHP, Muséum National d'Histoire Naturelle, Paris; MVM, Museum of Victoria, Melbourne; QM, Queensland Museum, Brisbane; QU, Entomology Department, University of Queensland, St. Lucia; SAM, South Australian Museum, Adelaide.

Baliomorpha gen. nov.

DESCRIPTION: Head with antennae moderately to very long, in males greater than $2\times$ length of forewing, in females shorter; vertex with a pair of large anterior warts usually extending to about half the width of eye, in place of posterior warts sometimes there is an elevated transversal ridge; frons flattened with scattered short setae; maxillary palpi long, segments 1 and 2 short, subequal, segment 3 about 3 to $4\times$ the length of segment 2. Forewing elongate, rounded apically, Sc forked at apex, cross-vein sc-c absent; discoidal cell small but not minute, median cell slightly larger than discoidal cell; thyridial cell very long, narrow, distal end tapered, nygma at about middle; forks 1-5 present, fork 1 usually sessile, or sometimes with short footstalk. Hindwing broad, wider in males, discoidal cell absent, fork 1 usually present, costal margin evenly curved. Abdominal sternite 5 without lateral filament; male genitalia with tergite X short, simple; inferior appendages undivided or nearly so. Female abdominal sternite VIII formed by a pair of lateral lobes, rounded and free standing distally; entirely separated mid-ventrally; tergite IX, in dorsal view, bluntly triangular, proximal margin gradually curved or broadly incised; some species with oval patch of short, stout bristles on either side of tergite; segment X terminates with three pairs of short processes, the ventral pair situated close to the middle pair (cerci) (Fig. 43). Spurs 1:4:4.

TYPE SPECIES: *Macronema pulchripenne* Tillyard 1922.

REMARKS: The genus is distinguished from *Macronema* and *Macrostemum* by the characters shown in the preceding table. Four Australian and five New Guinean species are included in the genus.

KEY TO SPECIES OF *Baliomorpha*

- 1 Australian species 2
- New Guinea species 5
- 2 Forewings with variable size yellowish to golden spots, mostly between veins; phallus in ventral view broad at base, expanded mid-laterally, apex narrowly spatulate *banksi*
- Forewings other than with small yellow or golden hairy spots; phallus, in ventral view, rounded at apex 3
- 3 Forewing blackish with single oblique golden or yellowish streak at pterostigma *urbana*

- Forewing brownish or with large yellow or golden spots 4
- 4 Forewing brownish with irregular pale longitudinal mark along thyridial cell and at anastomosis *dubia*
- Forewing with distinctive yellow to golden spots of variable size on blackish background colour *pulchripenne*
- 5 Forewing with two pale yellowish spots at midwing, anterior one triangular, posterior one somewhat rectangular (known from female type only) *loriai*
- Forewing with more than two spots 6
- 6 Forewing with pale yellowish transversal band across midwing, pale spot at pterostigma, indistinctly pale apical margin; phallus in ventral view apically expanded into lateral flanges *pezidion*
- Forewing with yellow spots merging into irregular pattern; in male genitalia, apex of phallus with dorsally directed chitinous points, in ventral view not expanded into lateral flanges 7
- 7 Distal margin of sternite IX extended into broad lobe; apex of phallus in ventral view somewhat angular *chiloma*
- Distal margin of sternite IX not extended into broad lobe; phallus in ventral view rounded apically 8
- 8 Lateral lobe of segment IX indistinct; phallus in ventral view long, slender, apex rounded *caudicea*
- Lateral lobe of segment IX distinct; phallus in ventral view gradually widened to elongate oval apex *echinata*

Baliomorpha pulchripenne (Tillyard 1922) comb. nov. Figs 1-3, 43, 44

- 1922 *Macronema pulchripenne* Tillyard, p. 83, pl. 24A, fig. 3.
1953 *Macronemum pulchripenne* (Tillyard); Mosely & Kimmins, p. 313, fig. 220.
1963 *Macronema pulchripenne* Tillyard; Fischer, p. 194.
1972 *Macronema pulchripenne* Tillyard; Fischer, p. 61.
1982 *Macrostemum pulchripenne* (Tillyard); Flint & Bueno-Soria, p. 369.

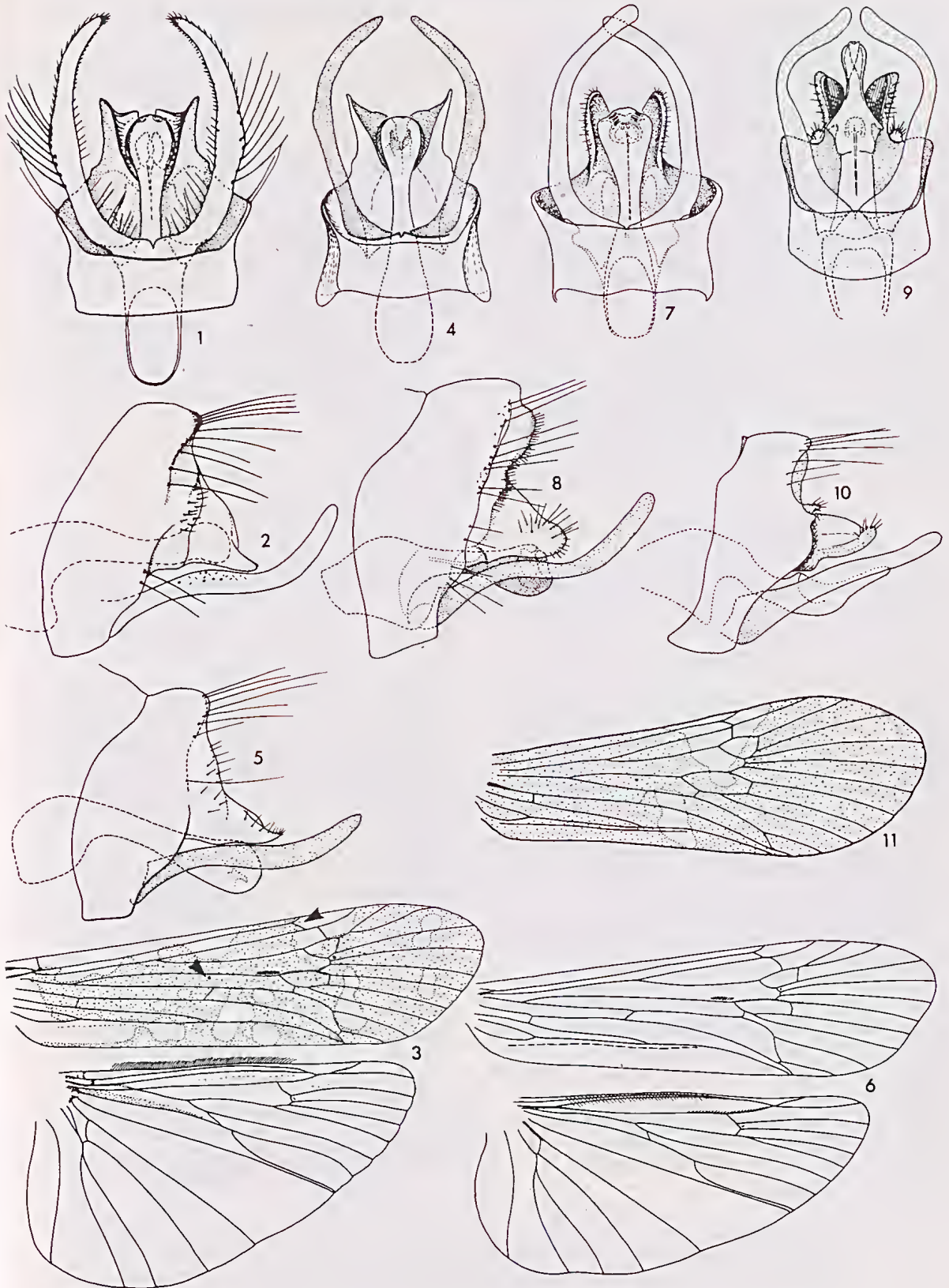
REMARKS: A distinctive Australian species with characteristic yellow to golden spots on blackish forewings, pattern somewhat variable. Male genitalia with segment X rather short, hood-shaped, lateral angles produced distally; phallus in ventral view straight, apex rounded, details as in Fig. 1.

Female abdominal tergite IX with oval mid-dorsal and elongate lateral patch of short setae; promixal margin evenly curved.

Length of anterior wing: ♂ ♀ 11-12.5 mm.

TYPE MATERIAL: Holotype ♀—New South Wales, Stanwell Park, 24 April 1916 (Lyell) (BMNH);

Figs. 1-11—*Baliomorpha* spp.: 1-3, *pulchripenne*; 1, male genitalia ventral; 2, lateral; 3, male, wing venation; 4-6, *urbana*; 4, male genitalia ventral; 5, lateral; 6, male, wing venation; 7-8, *dubia*; 7, male genitalia ventral; 8, lateral; 9-10, *banksi*; 9, male genitalia ventral; 10, lateral; 11, *loriai* (Navás, 1933), holotype female, forewing.



paratypes 2♀ same data, Cawthron Institute, New Zealand and Museum of Comparative Zoology, Harvard (not examined).

MATERIAL EXAMINED: New South Wales—1♀ Stanwell Creek, 23 April 1916 (label in G. Lyell's handwriting, undoubtedly one of the original series) (ANIC); 1♂ Colo Vale, 16 Jan. 1957, (Writh) (ANIC); 1♂ CSIRO Exp. farm Wilton, 8 May 1976 (Robinson) (ANIC); 1♂ Minnamurra Falls, 18 Dec. 1980 (Robinson) (ANIC); 1♂ Barrington Tops, 1400 m, 7 Dec. 1981 (Theischinger) (MVM); 1♀ Blundells, ACT, 6 Jan. 1961 (Riek) (ANIC). Victoria—1♂ Upper Buckland River, 30 Nov. 1964 (Neboiss) (MVM); 1♀ Snobs Creek, 15 Dec. 1955 (Hallgarten) (MVM); 7♀ Starvation Creek nr. Warburton, 22 Dec. 1976 (Dean and Cartwright) (MVM) (preparation PT-1327 figured); 2♂ 4♀ Cement Creek nr. Warburton, 22 Dec. 1976 (Dean and Cartwright) (MVM), (♂ genitalia preparation PT-694 figured); 1♀ Yea River, Gordon's Bridge, 6 Jan. 1954 (Neboiss) (MVM); 1♀ Eurobin Falls, Mt Buffalo Road, 3 Dec. 1982 (Neboiss) (MVM).

DISTRIBUTION: New South Wales; Victoria.

***Baliomorpha urbana* sp. nov.**

Figs 4-6, 39-41

REMARKS: The species was recognized, and the single female specimen briefly described, by Mosely and Kimmins (1953). However, no species name was given. Additional material, including males, is now available.

DESCRIPTION: The dark, blackish-brown forewings with pale, sometimes golden oblique spot at pterostigma distinguishes the species. The pale yellowish colour is present in wing membrane as well as in hair cover. Maxillary and labial palpi pale yellow, the same colour as the legs, except the mid- and hind coxae which are dark blackish brown. The contrasting golden yellow and blackish colours fade quickly in alcohol to become dull brown.

Male genitalia short, phallus rounded at apex, similar to that in *pulchripenne* but differing in details as shown in Fig. 4.

Female abdominal tergite IX with distinct lateral setose patches, mid-dorsal patch broad, indistinct; proximal margin curved (Figs 39, 40).

Length of anterior wing: ♂ ♀ 8-9 mm.

TYPE MATERIAL: Holotype ♂ SE Queensland, Mt Nebo, 13 Dec. 1959 (Kerr) (MVM T-8057); paratypes 11♂ 7♀ collected with holotype (ANIC; BMNH; MVM), genitalia preparations ♂ PT-693 and ♀ PT-1329 figured.

OTHER MATERIAL EXAMINED: SE Queensland—1♀ Mt Greville, 17 Aug. 1975 (Lambkin) (MVM); 1♂ Lamington Nat. Park 25 May 1983 (Yule) (MVM).

DISTRIBUTION: SE Queensland.

***Baliomorpha dubia* (Ulmer 1905) comb. nov.**

Figs 7, 8, 46, 47

1905 *Macronema dubium* Ulmer, p. 28, figs 15, 16

1907 *Macronema dubium* Ulmer; Ulmer, p. 103, fig. 107

1953 *Macronemum dubium* (Ulmer); Mosely & Kimmins, p. 308, figs 216, 217

1972 *Macronema dubium* Ulmer; Fischer, p. 159

1982 *Macrostemum dubium* (Ulmer); Flint & Bueno-Soria, p. 369.

REMARKS: Largest of the Australian species in the genus. Forewings brownish with pale brownish and yellowish markings mainly at midwing and near pterostigma; venation darker brown.

Male genitalia short, phallus gradually widened apically; inferior appendages slender, details as in Fig. 7.

Female abdominal tergite IX without lateral setose patches; proximal margin with broad, somewhat angular incision.

Length of anterior wing: ♂ 18-21 mm; ♀ 19-20 mm.

TYPE MATERIAL: Type ♂ 'Australia' without other data (MNHP) (not examined).

MATERIAL EXAMINED: SE Queensland—3♂ Browns Falls, Killarney, 13 Oct. 1973, Neboiss (MVM). New South Wales—16♂ 1♀ Boonoo Boonoo River, 11 Oct. 1973 (Neboiss) (MVM); (♂ genitalia preparation PT-1030 figured); 30♂ 16♀ Styx River 12 km S of Ebor, 17 Oct. 1973 (Neboiss) (MVM); 1♂ 18♀ Styx River, State Forest Camp, 28 Oct. 1981 (Wells and Carter) (MVM); 2♂ between Ebor and Dorrigo, 12 Nov. 1983 (Theischinger) (MVM); 2♀ Wilson River, Wauchope, 30 Oct. 1981 (Wells and Carter) (MVM); 1♂ Dorrigo Nat. Park, 20 Nov. 1973 (Moulds) (MVM); 1♂ Upper Allyn River, 8 Nov. 1960 (Common and Upton) (ANIC); 1♂ Minnamurra Falls, 16 Nov. 1960 (Common and Upton) ANIC; 1♂ 2♀ Upper Kangaroo Valley, 24 Nov. 1960 (Rick) (ANIC); 1♂ 48 km N of Singleton, 5 Oct. 1975 (Moulds) (MVM); 1♂ 2♀ Genova River, Rockton, 20 Nov. 1965 (Neboiss) (MVM) (♀ preparation PT-1328 figured). Victoria—1♂ Wonnangatta River, Hawkhurst 3 Dec. 1978, (Campbell) (MVM); 1♂ Cann River, Buldah, 17 Dec. 1976 (Neboiss) (MVM); 1♂ 1♀ Macalister-Barkly River Junction, Lyndon Flats, 6 Dec. 1977 (NMV Survey Dept.) (MVM).

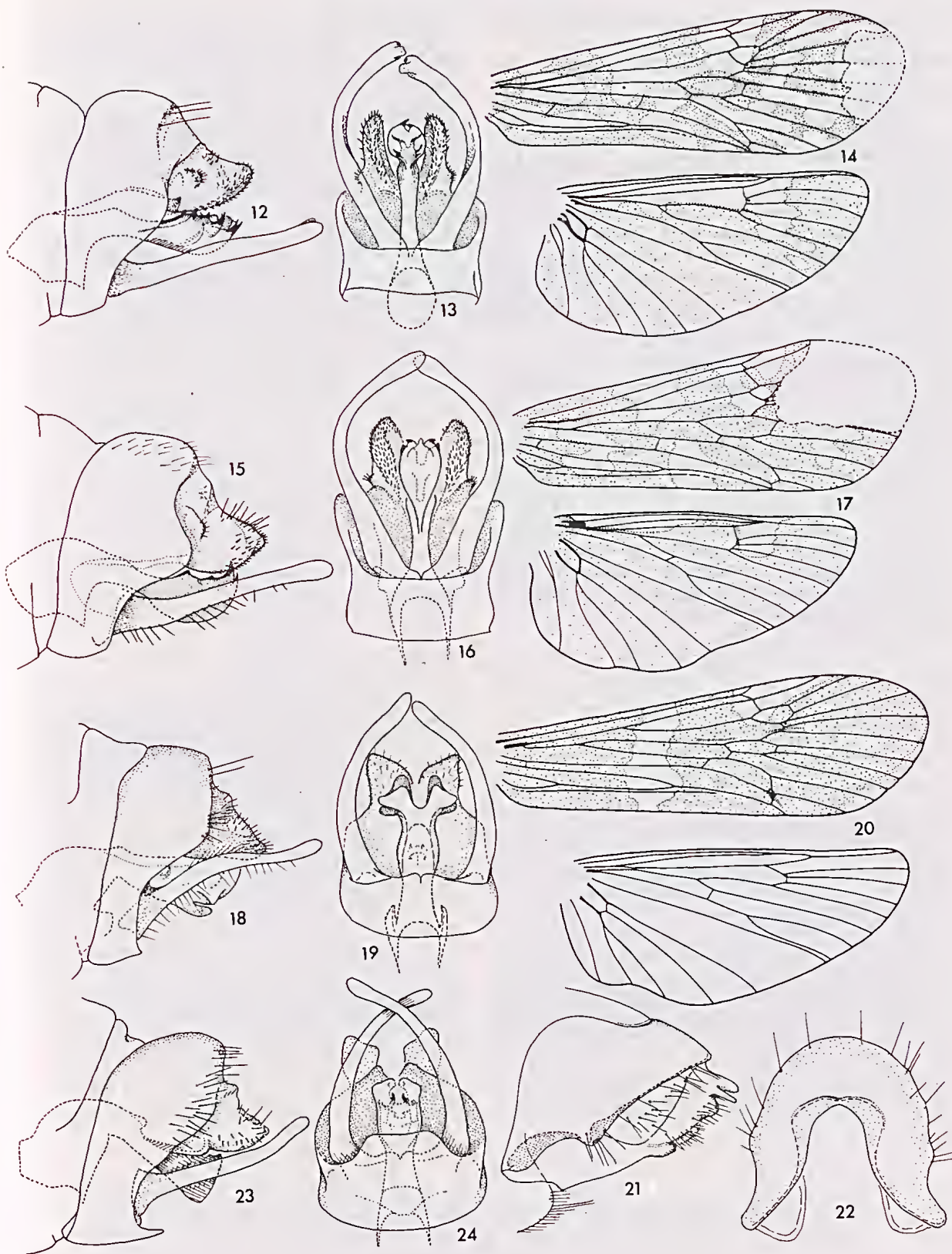
DISTRIBUTION: SE Queensland, E New South Wales, E Victoria.

***Baliomorpha banksi* (Mosely 1953) comb. nov.**

Figs 9, 10, 35-38

1939 *Macronema tristis* Banks, (non *triste* Navás) p. 487 figs 58, 61.

Figs. 12-24—*Baliomorpha* spp.: 12-14, *caudicea*, holotype; 12, male genitalia lateral; 13, ventral; 14, wing venation; 15-17, *echinata*, holotype; 15, male genitalia lateral; 16, ventral; 17, wing venation; 18-22, *pezidion*; 18, male genitalia lateral; 19, ventral; 20, female (PT-1284), wing venation; 21, female, apex of abdomen lateral; 22, dorsal; 23-24, *chiloma*, holotype; 23, male genitalia lateral; 24, ventral.



1953 *Macronemum banksi*, Mosely in Mosely and Kimmins, p. 312 fig. 219.

1964 *Macronemum torrenticola* Korboot, p. 39 figs 58-78, syn. nov.

1982 *Macrostemum banksi* (Mosely); Flint & Bueno-Soria, p. 369.

REMARKS: According to the International Zoological Rules the species names replaced before 1960 due to preoccupation retain their status when transferred to another genus, therefore the replacement name *banksi* remains valid within the new genus *Baliomorpha*.

The species has two main areas of distribution, one in North Queensland associated with rainforests between Iron Range and Cairns, the other in the mountainous regions in SE Queensland. In both areas the species occur in small, rapidly flowing streams.

It is characterised by having dark, blackish wings, covered with numerous pale yellowish to golden irregular spots, mostly scattered between the veins and usually formed by golden pubescence. However, some spotting is also present on the wing membrane. Females usually are slightly smaller, their wings less ornate.

Head (Fig. 38), compared with that in *saundersi* rather short and broad, anterior warts large; palpi and legs brownish-grey; maxillary palpi with segment 5 longer than segments 1-4 together. The 'forked' tip of 'penis' as illustrated in the original figures (Banks 1939) apparently developed in the drying process. Phallus, in ventral view, expanded mid-laterally, apex upcurved, slightly spatulate.

Female abdominal tergite IX with lateral setose patches on oval translucent areas (Figs 35, 36), mid-dorsal setal patch absent, proximal margin with deep angular incision.

Length of anterior wing—♂ 9.5-11.5 mm; ♀ 7.5-8.5 mm.

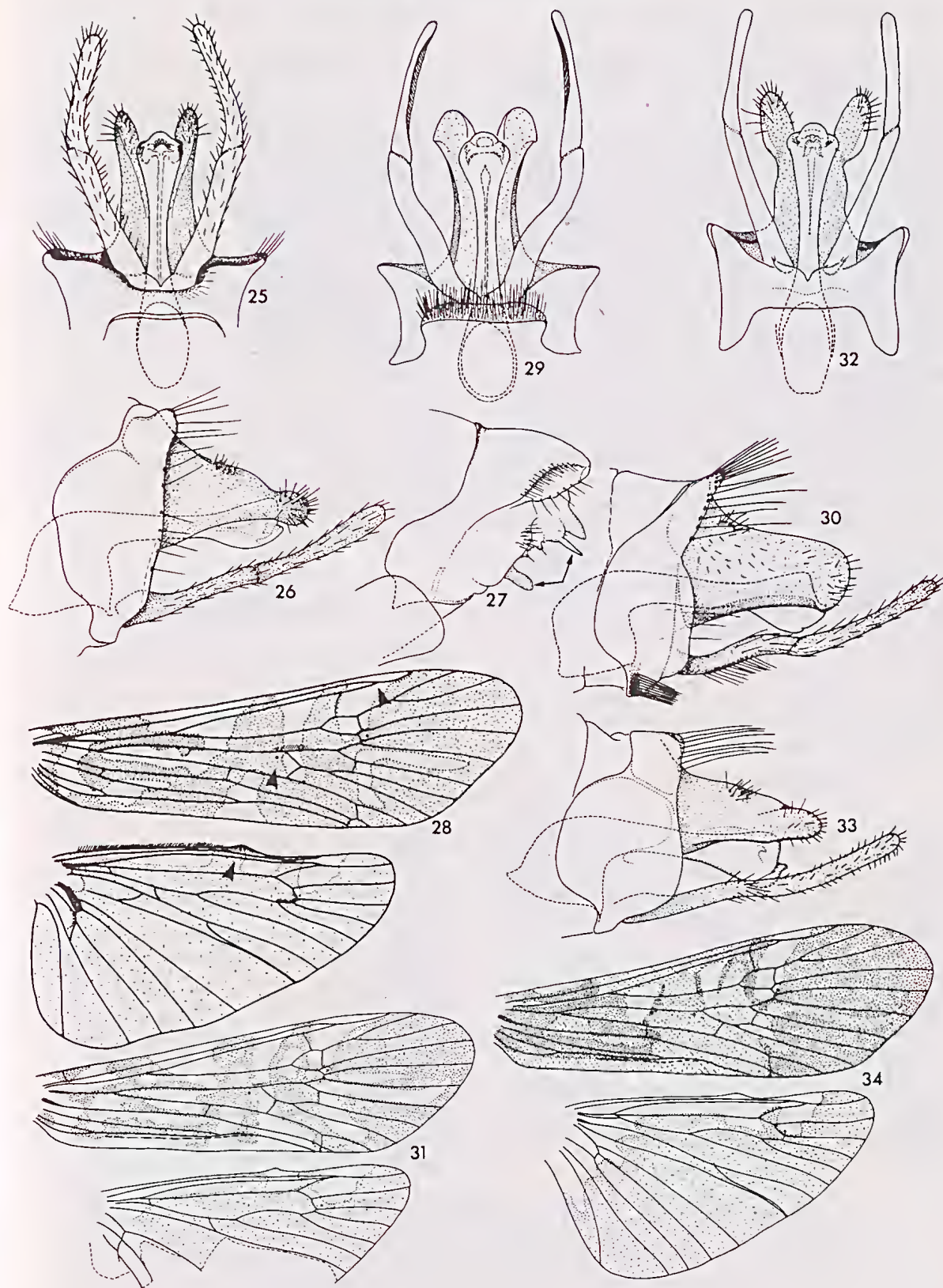
TYPE MATERIAL: Holotype ♂ of *Macronema tristis* Banks—Queensland, Atherton Tableland, Ravenshoe, 27 April (1932) (Darlington) (MCZ now transferred to ANIC); paratypes 2♂, North Queensland, Rock Scrub, McIlwraith Range, 17-29 June (1932) (Darlington) (MCZ now transferred to ANIC). Types examined. Type of *Macronemum torrenticola* Korboot: Holotype ♂ in alcohol with right side wings and abdomen removed; in the same vial one ♀ with head and right side wings detached and loose in vial; there is also present a cast pupal shell and the following labels: 'Montville, Q. Mar. 1962 K.K. sp.R/*macronemum* sp. nov. E. F. Riek det. 1962/*M. torrenticola* ♂ Holotype Korboot/QM reg. number ♂ Holotype T-6183; ♀ paratype T-6184'. The two microscope slides bearing the name *M. torrenticola* Holotype ♂, Korboot (in her handwriting) give

the locality 'Cedar Creek, Tamborine Mts. Q. 3 Oct. 1962'. The slide with wings reg. number T-6183a is of this species; the slide T-6183b however, contains the abdomen of *Smicrophylax* sp. ♂.

MATERIAL EXAMINED: N. QUEENSLAND—3♂ Mt Tozer, Iron Range 30 April 1973 (Monteith) (ANIC); 4♂ Cap Creek, Mt Finlayson Range S of Cooktown 23 Nov. 1974 (Moulds) (ANIC); 17♂ ♀ Mossman Gorge, 23 April 1967 (Colless) (ANIC); 7♂ same loc. 16 Nov. 1979 (Neboiss) (MVM); 2♂ Cape Tribulation, Nov. 1982 (Hinger) (MVM); 1♂ Mt Lewis Road off Mossman-Molloy road, 22 April 1967, (Colless) (ANIC); 1♀ Kuranda, 30 Mar. 1976 (Quick) (MVM); 1♂ Currunda Creek, Freshwater Creek tributary, Cairns district, 30 April 1979 (Wells) (MVM); 1♂ N Toohey Creek, Lake Barrine, 14 May 1936 (no collector) (ANIC); 1♂ 8 km N Bloomfield River, 7-9 May 1978 (Curtis) (ANIC); 1♂ Cairns May 1963 (Korboot) (QU); 5♂ Mt Edith Forest Road, 1.5 km off Danbulla Road, 6 May 1967 (Colless) (ANIC); 1♂ Whitfield Range forest reserve, Cairns 19 April 1967 (Colless) (ANIC); 8♂ 2♀ Fishery Falls, S of Gordonvale 29 June 1971 (Riek) (ANIC; MVM) (♂ genitalia preparation PT-678 figured); 4♂ 1♀ Mulgrave River W of Gordonvale, 29 April 1979 (Wells) (MVM); 1♂ 14♀ Little Mulgrave River 9 km SW of Gordonvale 17 Nov. 1979 (Neboiss) (MVM) (♀ preparation PT-1194 figured); 6♂ 1♀ same loc. 28 June 1971 (Riek) (ANIC); 2♂ The Boulders, Babinda 10 May 1967 (Colless) (ANIC); 1♂ Josephine Falls, SW of Babinda 15 Nov. 1979 (Neboiss) (MVM); 16♂ The Boulders, Babinda Creek 18 Nov. 1979 (Neboiss) (MVM); 2♂ Mt Bartle Frere 29 May 1963 (Shaw) (QU); 13♂ 25 km Gordonvale, Gillies H-way 4 Sept. 1979 (Moulds) (MVM); 6♂ Killama State Forest, 31 May 1971 (Riek) (ANIC); 1♂ Dinner Falls via Ravenshoe, May 1963 (Korboot) (QU); 1♀ Little Cedar Creek, nr. Townsville, 31 Jan. 1965 (no coll.) (QM); 1♂ Broken River, Eungella Nat. Park. 24 April 1979 (Wells) (MVM); 8♂ 35 km SW Ingham 30 May & 5 June 1961 (Straatman) (ANIC; MVM); 2♂ Finch Hatton Gorge, 60 km W of Mackay 14 Nov. 1982 (Hinger) (MVM). SE Queensland—1♂ Brookfield, 10 May 1964 (Dunwoody) (QU); 3♂ 2♀ Highvale 22 km NW of Brisbane 29 Nov. 1959 (Straatman) (ANIC; MVU); 3♂ same loc. April 1963 (Hunter) (QU); 2♂ Dawson Creek Highvale 6 Mar. 1963 (Breedon) (QM); 1♂ 2♀ Ashgrove nr. Brisbane, Aug. 1960 (Korboot) (QU); 1♂ Cedar Creek Falls, Mt Tamborine 23 Feb. 1963 (Breedon) (QM); 3♂ same loc. Mar. 1962 (Korboot) (QU); 1♀ Tcviot Brook nr. Wilson's Peak, 153°31'E 28°13'S, 17 Nov. 1980 (Daniels & Schneider) (QU).

DISTRIBUTION: N and SE Queensland.

Figs. 25-34—*Macrostemum* spp.: 25-28, *saundersi*; 25, male genitalia ventral, holotype; 26, lateral; 27, female, apex of abdomen lateral (PT-1197, from Australia); 28, male wing venation (from Cape York, Australia); 29-31, *loriai* (Navás, 1930); 29, male genitalia ventral (PT-1244); 30, lateral; 31, male wing venation (PT-1244); 32-34, *auriferum*, holotype; 32, male genitalia ventral; 33, lateral; 34, male wing venation.



Baliomorpha lorai (Navás 1933) comb. nov.

Figs 11, 48

1933 *Macronema lorai* Navás (non 1930) p. 42, fig. 94
 1982 *Macrostemum lorai* (Navás); Flint & Bueno-Soria, p. 369.

REMARKS: There has been confusion in the past over the identity of the two species described in 1930 and 1933 under the same name and it was, therefore, important to re-examine both the type specimens, which were made available for this study by the Museum Giacomo Doria at Genova. Kimmins (1962) noted that *Macronema lorai* Navás 1930 is not the same species as *Macronema lorai* Navás 1933. In this revision these two species are placed in separate genera, the one described in 1930 is referred to *Macrostemum*, the other, described in 1933, to *Baliomorpha*. Thus both can retain their original species names.

Unfortunately the abdomen of the type female has been somewhat distorted (Fig. 48) in the drying process, nevertheless the close distance between cerci and lower tubercle pair, together with the wing venation, provide sufficient information for placement in the genus *Baliomorpha*. It should also be noted that the original illustration (Navás 1933, fig. 94) shows the forewing inverted with costa towards the bottom of page.

Female abdomen with distal margin of sternite VIII formed by two mesally separated lobes, segment IX in lateral view subtriangular; there appear to be no lateral setose patches present. Length of anterior wing ♀ 8.8 mm. Male unknown.

TYPE MATERIAL: Holotype ♀: 'New Guinea Mer.' without exact locality and date; collector L. Loria (MCG), preparation and forewing PT-1283 figured.

DISTRIBUTION: E New Guinea.

Baliomorpha caudicea sp. nov.

Figs 12-14

DESCRIPTION: Head vertex dark brown except for yellow lateral patch on anterior warts; posterior-transversal ridge interrupted at mid-line, frons and antennae yellow; forewing with extensive yellow pattern as shown in figure 14, distal section of veins beyond anastomosis accented with dark brown colour.

Male genitalia tergite X covered with scattered stout spines; inferior appendages with a small apical lobe; phallus in ventral view slender proximally, apex dilated, rounded with dorsally directed spines.

Length of anterior wing ♂ 12 mm. Female unknown.

TYPE MATERIAL: Holotype ♂ New Guinea: (Papua New Guinea) S Garaina 900-1800 m/8-14 Jan. 1968/ (Sedlacek) (BPBM), genitalia preparation and wings PT-1243 figured.

DISTRIBUTION: E New Guinea.

Baliomorpha echinata sp. nov.

Figs 15-17

DESCRIPTION: Head vertex entirely yellow, posterior transversal ridge broad, interrupted at mid-line, frons and antennae yellow, covered with dark pubescence; forewing (Fig. 17) with bold yellow blotches as illustrated, there is some darkening along veins. However, not as distinctive as in *caudicea*, also the pale areas are less extensive.

Male genitalia (Figs 15, 16) similar to *caudicea* with short scattered spines on apex and lower ridge of tergite X; inferior appendages smoothly rounded at apices; phallus gradually dilated apically with several dorsally directed spines.

Length of anterior wing ♂ 10.7 mm. Female unknown.

TYPE MATERIAL: Holotype ♂ New Guinea: (Papua New Guinea), Finnhafen 13 Apr. (no year) (Sedlacek) (BPBM), genitalia preparation and wing venation PT-1220 figured; 1 ♂ paratype Wareo, Finnhafen (Rev. Wagner) (SAM).

DISTRIBUTION: E New Guinea.

Baliomorpha pezidion sp. nov.

Figs 18-22

DESCRIPTION: Head with vertex distinctly bicolorous— anterior half blackish brown, posterior half, anterior warts and frons yellow, colour division along the elevated transversal ridge which is continuous across mid-line. Forewing (Fig. 20) with transverse pale yellow band at midwing and an elongate triangular spot at anastomosis, including part of discoidal cell; less distinct pale yellow colour is also present along the apex of the wing and at anal area.

Male genitalia (Figs 18, 19) with tergite X, in lateral view, short, triangular, ventral surface with scattered bristles; phallus deeply incised at apex, with two pairs of lateral lobes.

Two females from the same general area are provisionally referred to this species; in both specimens the yellow wing markings are more restricted than in the male, particularly along the anal margin. Abdominal tergite IX without lateral setose patches, proximal margin deeply incised mid-dorsally (Fig. 22).

Length of anterior wing ♂ ♀ 7.5 mm.

TYPE MATERIAL: Holotype ♂ New Guinea: (Papua New Guinea) Wau 1260 m 14 May 1965 (Sedlacek) (BPBM); without left forewing; holotype genitalia preparation PT-1223 figured.

Figs. 35-48—35-38, *Baliomorpha banksi*; 35, female, apex of abdomen lateral; 36, dorsal; 37, ventral; 38, male head, dorsal; 39-41, *Baliomorpha urbana*; 39, female, apex of abdomen lateral; 40, dorsal; 41, male head, dorsal; 42, *Macrostemum saundersi* holotype male, head dorsal; 43-44, *Baliomorpha pulchripennis*; 43, female, apex of abdomen lateral; 44, dorsal; 45, *Macrostemum zebratum* male head dorsal; 46-47, *Baliomorpha dubia*; 46, female, apex of abdomen lateral; 47, dorsal; 48, *Baliomorpha lorai* (Navás, 1933) holotype female, apex of abdomen ventral.

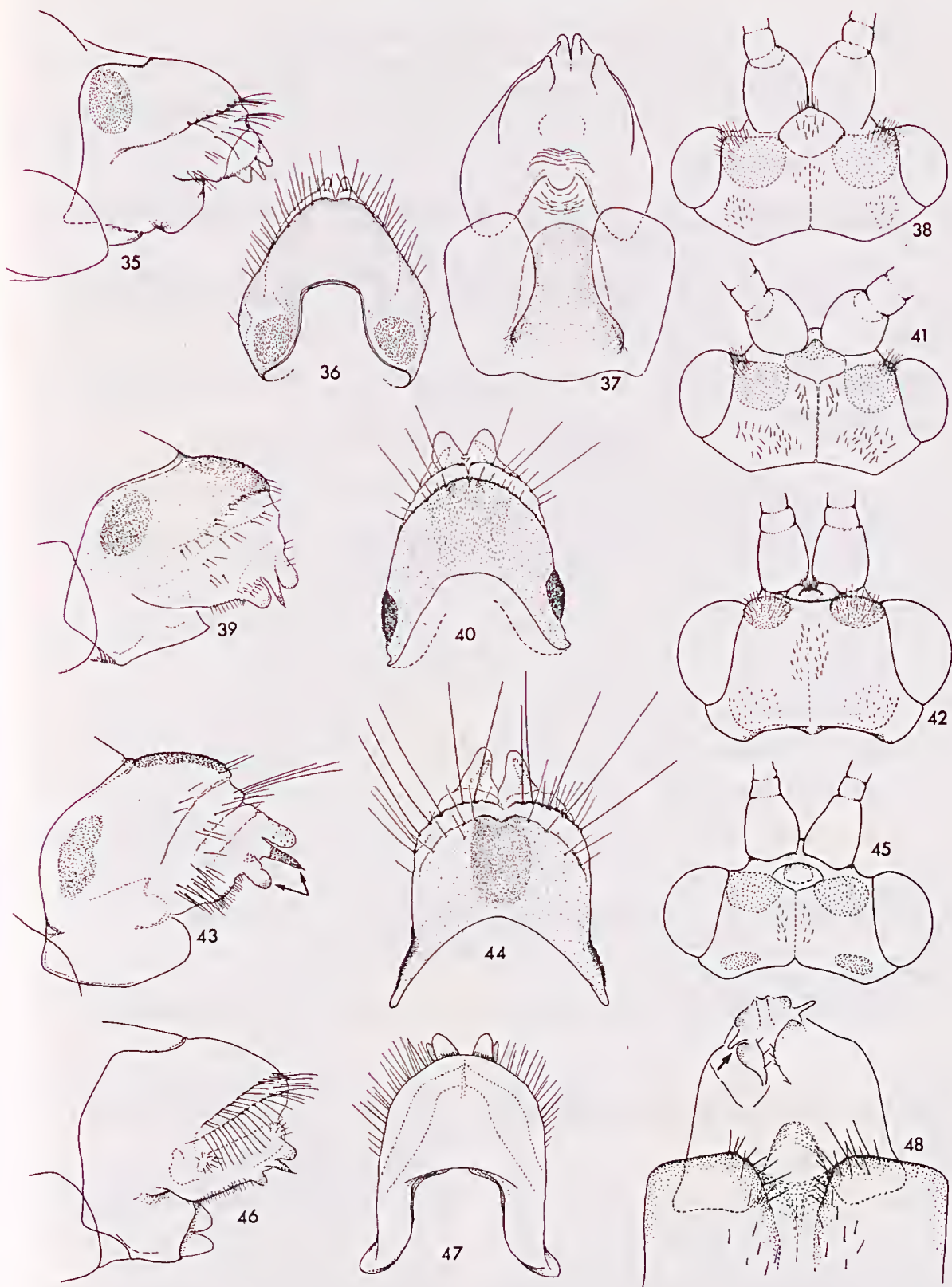


TABLE 1
CHARACTER STATES SEPARATING *MACRONEMA* AND *BALIOMORPHA*

	<i>MACRONEMA</i> (Neotropical)	<i>BALIOMORPHA</i> (Australia, New Guinea)
HEAD:		
frons	without elevated pad	without elevated pad
warts on vertex	anterior pair large; posterior pair absent	anterior pair large; posterior pair absent
maxillary palp	segments 1 and 2 short, subequal; segment 3 very long	segments 1 and 2 short, subequal; segment 3 very long
SPURS:	0:4:4	1:4:4
ABDOMINAL STERNITE V	without lateral filament	without lateral filament
MALE GENITALIA:		
tergite X	short, broad, often with lobes or processes	short, simple
inferior appendages	undivided or nearly so	undivided
apex of phallus	often with lobes and processes	rounded, sometimes with lobes or spines
FOREWING:		
Sc	ending on costa	forked at end
cross-vein sc-c	one	absent
discoidal cell	minute	small
nygma of thyridial cell	at about middle of cell	at about middle of cell
distal end of thyridial cell	narrow	narrow
colour	dense, mostly due to scales	scale cover moderate to dense, colour due to scales or in membrane
HINDWING:		
costal margin	evenly curved	evenly curved
FEMALE		
ABDOMINAL SEGMENT X:		
distance between cerci and lower tubercle pair	(?)	less than length of tubercle

MATERIAL EXAMINED: New Guinea: (Papua New Guinea): 2 ♀ Wau, 1200 m. 22 Oct. 1965 (Sedlacek) (BPBM).

DISTRIBUTION: E New Guinea.

***Baliomorpha chiloma* sp. nov.**

Figs 23-24

DESCRIPTION: Head vertex dark brown except posterior margin which is yellowish, without posterior transversal ridge, frons yellow, antennae with scape yellowish,

subsequent segments become gradually darker; forewing dark brown except for a pale ovoid patch at costal margin near discoidal cell.

Male genitalia (Figs 23, 24) with segment IX produced mid-ventrally into a short, broad lobe, phallus apically somewhat angular with circular mesal incision, and a pair of dorsally directed, curved spines.

Length of anterior wing ♂ 8.5 mm. Female unknown.

TYPE MATERIAL: Holotype ♂: New Guinea: (Irian Jaya) Bokondini, 40 km N of Baliem Val. ca 1300 m, 16-23

TABLE 2
CHARACTER STATES SEPARATING *MACROSTEMUM* GROUPS

	<i>MACROSTEMUM</i> (N America, Africa)	<i>MACROSTEMUM</i> (Australia, New Guinea)
HEAD:		
frons	without elevated pad	with elevated setose pad
warts on vertex	anterior pair of medium size, posterior pair present, small to medium	anterior pair present, medium size, situated well forward, posterior pair absent
maxillary palp	segments 1 and 2 short, 3 slightly to distinctly longer than 2	segment 1 shorter than 2, 3 only slightly longer than 2
SPURS:	1:4:4 or 2:4:4	2:4:4
ABDOMINAL STERNITE V	without lateral filaments (filaments present in males of African species)	lateral filaments present in both sexes
MALE GENITALIA:		
tergite X	elongate, simple	elongate, simple
inferior appendages	distinctly 2-segmented	2-segmented, division indistinct
apex of phallus	generally bulbous, without special structures	bulbous
FOREWING:		
Sc	united with R ₁ apically or ending in fork whose ventral arm united with R ₁	united with R ₁ apically
cross-vein sc-c	several indistinct or none	absent
discoidal cell	small	small
nygma of thyridial cell	at distal end	at distal end
distal end of thyridial cell	broad	broad
colour	contrasting colour of membrane, scale cover sparse (setose, not scaly in African species)	contrasting colour of membrane, accented by cover of fine, dense pubescence
HINDWING:		
costal margin	excised before apex or evenly curved	excised before apex
FEMALE, ABDOMINAL SEGMENT X:		
distance between cerci and lower tubercle pair	greater than length of tubercle	greater than length of tubercle

Nov. 1961 (Quate) (BPBM), genitalia preparation PT-1219 figured.

DISTRIBUTION: W New Guinea.

Macrostemum Kolenati 1859

TYPE SPECIES: *Macronema hyalinum* Pictet (designated by Ulmer 1957, p. 339).

REMARKS: The generic diagnosis given by Flint and Bueno-Soria (1982) is based on typical North American species. Some amendments were made by Scott (1983) to include African species. Table 2 summarizes the different character states existing between the North American-African and the Australian-New Guinean species groups. The following generic diagnosis is

modified and refers to species of the Australian and New Guinea region only.

Head with antennae long, in males $2\times$ length of forewing, in females shorter; vertex with a pair of moderate size anterior warts, situated close to the base of antennae, posterior pair of warts present in N-American species (Fig. 45). Frons with distinct elevated setose pad immediately below the base of antennae (not present in American or African species); maxillary palpi with segment I shorter than segment 2; segment 3 only slightly longer than 2. Forewing colour pattern present in wing membrane, accented by fine dense pubescence; costal cross-veins absent, Sc united with R_1 before wing margin; discoidal cell small but not minute, median cell larger than discoidal cell, thyridial cell long, nygma close to the rather broad distal end, forks 1-5 present, fork 1 with footstalk. Hind wing broad, costal margin excised before apex, partially bordered with hooked macrotrichia. Abdominal sternite V with lateral filament present in both sexes; male genitalia with tergite X comparatively slender, elongate; inferior appendages indistinctly divided in two segments; apex of phallus bulbous.

Female abdominal sternite VIII formed by a pair of elongate lateral lobes, rounded and free standing distally, separated mid-ventrally; tergite IX in dorsal view bluntly triangular, proximal margin gradually curved; segment X terminates with three pairs of short tubercles of which the ventral pair is separated from the middle ones (cerci) by a distance equal to, or greater than the length of a tubercle. Tibial spurs in both sexes 2:4:4.

At present only 3 Australian-New Guinean species (*saundersi*, *auriferum* and *loriai*) are referred to this group. Published information indicates that a number of other species of the Sunda Archipelago may belong here.

Macrostemum saundersi (McLachlan 1866)

Figs 25-28, 42

1866 *Macronema saundersii* McLachlan, p. 261, pl. 17, fig. 3; pl. 19, fig. 4.

1907 *Macronema saundersii* McLachlan; Ulmer, p. 103

1982 *Macrostemum saundersi* (McLachlan); Flint & Bueno-Soria, p. 369

REMARKS: The species is recognized by its distinct forewing pattern (Fig. 28) and details of male genitalia. The pale yellow areas in forewing are similar, but less extensive than in *loriai*.

Male abdominal segment IX rather broad dorsally; segment X in lateral view slender, tapering distally, in ventral view both lobes slightly divergent, gradually tapered to evenly rounded apices.

Length of anterior wing: σ 10-11.5 mm; ϕ 10-11 mm.

TYPE MATERIAL: Holotype σ loc. 'M' = Misool (Irian Jaya) (BMNH) genitalia preparation in glycerine, illustrated.

MATERIAL EXAMINED: New Guinea—1 σ Wau, Morobe district 1200 m 26 Oct. 1961 (Sedlacek) (PT-1242)

(BPBM), 1 ϕ 14.4 km W Lae 28-30 Oct. 1965 (Steffan & Huang) (BPBM). N Queensland—3 ϕ Bamaga, Cape York 30 Mar. 1964 (Common & Upton) (ANIC); 50+ σ ϕ Upper Jardine River (9 stations) 10-27 Oct. 1979 (Moulds) (MVM) (σ wings figured); 1 σ Claudie River (Iron Range) 20 May 1961 (Kerr) (MVM); 1 ϕ Iron Range 10 April 1964 (Common & Upton) (ANIC); 20+ σ ϕ Middle Claudie River Iron Range, 21 Sept.-23 Oct. 1974 (Moulds) (MVM) (ϕ genitalia preparation PT-1197 figured); 20+ σ ϕ Gordon Creek, Iron Range 18 April-1 June 1975 (Moulds) (MVM); 25+ σ ϕ Melvor River N of Cooktown, 4 Jan. 1981 (Moulds) (MVM); 1 σ same loc. 15 Feb. 1982 (Moulds) (MVM); 1 ϕ 3.5 km S of Mt Lamond, Iron Range, 22 Dec. 1971 (McAlpine and Holloway) (AM).

DISTRIBUTION: New Guinea, N Australia (Cape York Peninsula).

Macrostemum auriferum sp. nov.

Figs 32-34

DESCRIPTION: A dominating golden coloured transverse band in the centre of anterior wing (Fig. 34), incorporating some small paler areas distinguishes this species.

Head black with metallic bluish lustre, anterior warts small, orange-brown.

Male genitalia (Figs 32, 33) similar to *saundersi*, but lobes of segment X in ventral view with distinct constriction before club shaped apices.

Females show the same colour pattern on wings as males.

Length of anterior wings: σ 9.5-11 mm; ϕ 10-11 mm.

TYPE MATERIAL: Holotype σ New Guinea (Irian Jaya) Bodem, 100 m 11 km SE Of Oerberfaren 10-17 July 1959, Maa) (BPBM) σ abdomen preparation PT-1218 figured; right side wings dry mounted and figured. Paratypes 4 ϕ collected with holotype (BPBM).

MATERIAL EXAMINED: New Guinea (Irian Jaya) 2 ϕ Nabire 5-50 m. 25 Aug.-20 Sept. 1962, Light trap in jungle (Holtman) (BPBM).

DISTRIBUTION: W New Guinea.

Macrostemum lorlai (Navás 1930)

Figs 29-31

1930 *Macronema lorlai* Navás (not Navás 1933) p. 22, fig. 4

1962 *Macronema lorlai* Navás; Kimmins, p. 135

1982 *Macrostemum lorlai* (Navás); Flint & Bueno-Soria, p. 369

DESCRIPTION: Wing pattern similar to *saundersi*, but with yellow areas more extensive, and postero-apical mark along fork 3 tapered and extended into fork 2 at wing margin; a parallel mark is present between forks 2 and 3.

Abdomen with lateral process on sternite V long, robust, basal half thickened; hind tibia covered with fine long hairs. Male genitalia in lateral view with segment X

rather broad apically, postero-ventral margin of sternite IX densely covered with stiff bristles.

Length of anterior wings: ♂ ♀ 12-13 mm.

TYPE MATERIAL: Type ♂, New Guinea (Papua New Guinea) Haveri (147°35'E, 9°25'S, alt. 600 m. Astrolabe Mts) July-Dec. 1893; coll. by Loria (MCG) (type examined).

MATERIAL EXAMINED: New Guinea—1 ♂ Papua New Guinea, Lae, Singuawa Riv. 147°35'E, 6°45'S 30 m. 11 April 1966 (Wilkes) (BPBM) (♂ genitalia preparation PT-1244 figured), (wings mounted and figured); 1 ♂ Mt Lamington/NE Papua/1300-1500 ft. (McNamara) (SAM); 1 ♂ Wareo, Finnhafen New Guinea Rev. L. Wagner (SAM). Recorded by Kimmins (1962): 16 ♂ 3 ♀ Kokoda and 1 ♂ 4 (sex?) from Lake Sentani, Ifar (Irian Jaya) (specimens not seen).

DISTRIBUTION: New Guinea.

ACKNOWLEDGEMENTS

The author is indebted to Dr P. C. Barnard of the British Museum (Natural History) London for confirming synonymies and loan of specimens; Dr R. Pogany of the Museo Civico di Storia Naturale, Genova for the loan of Navás type specimens and to Ms J. Cardale of the Australian National Insect Collection, Canberra for the loan of type specimens and other important material. Greatly appreciated were comments to the manuscript by Mrs A. Wells, Zoology Department, University of Adelaide, Dr T. R. New, LaTrobe University, Bundoora, Mr J. C. Dean of MMBW Laboratories, Melbourne and Mr K. L. Walker of Entomology Department, Museum of Victoria.

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IMMATURE STAGES OF *BALIOMORPHA PULCHRIPENNE*
(TILLYARD) FROM AUSTRALIA, WITH COMMENTS ON
GENERIC PLACEMENT (TRICHOPTERA:
HYDROPSYCHIDAE)

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ABSTRACT: The larva and pupa of *Baliomorpha pulchripenne* (Tillyard) from southeastern Australia are described, and generic placement of the species is discussed. The close affinity with the larva of the neotropical species *Macronema variipenne* Flint & Bueno is emphasised. However, differences between larvae of the Australian and the South American species support the transfer of Australian species to a separate genus.

The subfamily Macronematinae is widely distributed, with species recorded from all continents. Australian species have until recently been referred to the genera *Aethaloptera* Brauer and *Macronema* Pictet (Neboiss 1983). The genus *Aethaloptera* is represented by a single species, *A. sexpunctata* (Kolenati), which has only been recorded from north Queensland and is clearly a northern element of the Australian fauna (Barnard 1980). The type species of the genus *Macronema* is *M. lineatum* Pictet from Brazil. The larva of another neotropical species, *M. variipenne* Flint & Bueno, has recently been described by Flint and Bueno (1982). These authors, after consideration of both adult and larval morphology, redefined the genus *Macronema*, restricting it to twenty-six listed neotropical species. They resurrected the genus *Macrostemum* Kolenati to accommodate additional neotropical species, as well as all species from North America, Africa, Asia and Australia, which had previously been referred to the genus *Macronema*. Neboiss (1984), however, has now revised the taxonomy of Australian species, and has established the genus *Baliomorpha* to accommodate them. In addition he has recorded from northern Australia the species *sandersi* McLachlan, previously only known from New Guinea, and has referred it to the genus *Macrostemum*.

Larvae of Australian Macronematinae have not been formally described, although whole larvae have been figured as 'Macronematinae' (Riek 1970) and 'Genus J' (Cartwright & Dean 1982). Korboot (1964) has described and figured a larva which she identified as *Macronemum torrenticola* Korboot. However, her figures clearly show that she has misassociated the larva, which is in fact a species of the subfamily Dipletroninae. The larva of *B. pulchripenne* (Tillyard) from Victoria has now been bred through to the adult, and is described below, thus allowing some comment on generic placement of Australian species.

SYSTEMATICS

Baliomorpha pulchripenne (Tillyard 1922)

Figs 1A-E, 2A-E

1922 *Macronema pulchripenne* Tillyard, p. 83, pl. 24A, fig. 3.

1953 *Macronemum pulchripenne* (Tillyard); Mosley & Kimmins, p. 313, fig. 220.

1963 *Macronema pulchripenne* Tillyard; Fischer, p. 194.

1984 *Baliomorpha pulchripenne* (Tillyard); Neboiss, p. 128, figs 1-3, 43, 44.

DISTRIBUTION: *Baliomorpha pulchripenne* has only been recorded from Victoria and New South Wales, and is apparently restricted in distribution to southeastern Australia.

DESCRIPTION: Larva. Length 20 to 22 mm, width 2.5 mm. Head and thoracic sclerites golden-brown. Head slightly longer than wide (Fig. 1B). Frontoclypeus with anterior margin concave, somewhat asymmetrical; no prominent knobs near anterolateral corners. Setae on frontoclypeus short, restricted to anterolateral corners and one or two near apex. Genae with numerous short, sharp setae and scattered long setae on anterior two-thirds only. Ventral surface of head with two rows of medium length setae near anterior margin (Fig. 1C). Stridulatory grooves absent. Anterior ventral apotome not fully delimited, ecdysial line absent on right side. Posterior ventral apotome very small. Labrum hairy on anterior half, without anterolateral brushes. Mandibles short, robust, without well developed teeth (Fig. 1E). Pronotum with transverse sulcus (Fig. 1A); numerous setae anterior to sulcus. Prosternite crescent-shaped with mesal projection on anterior margin; posteriorly a smaller triangular sclerite, with lateral angles extended into blunt arms (Fig. 2A). Mesonotum and metanotum with numerous setae, both short and long. Thoracic gills absent. Foretrochantin blunt, with numerous setae. Fore coxa long, also with numerous setae (Fig. 2B). Femur broad, with ventral row of stout peg-like setae; palmate setae not present on femur. Tarsus less than half length of tibia. Mid and hind legs with coxa, trochanter and femur elongate, all segments with numerous long setae, and without short peg-like setae (Fig. 2C). Tarsus without apico-dorsal spine. Gills on abdominal segments 1 to 7; each filament feather-like with numerous lateral branches (Fig. 1A). Gill formula as in Table 1. Abdominal segments clothed with short setae. Scattered long setae dorsally, and a cluster of

TABLE 1
SCHEMATIC GILL DIAGRAM OF THE LATERAL ASPECT OF MESO- AND METATHORAX
AND FIRST EIGHT ABDOMINAL SEGMENTS

	Meso	Meta	1	2	3	4	5	6	7	8
<i>Baliomorpha pulchripenne</i> Australia			D	DD	DD	DD	DS	DS	DS	
<i>Macronema variipenne</i> Neotropics (After Flint & Bueno 1982)			D	DD	DD	DD	SS	SS	S	

S = single central stalk

D = two S-type stalks with adjacent bases

medium length setae posterior to the gill filaments. Sternum 9 with numerous long setae; centrally a pair of small sclerites bearing fewer than ten short, stout spines (Fig. 1D). Anal gills absent. Anal prolegs long and slender, not bent at midlength. Anal claws slender and curved.

Pupa. Length about 10 mm. Labrum with anterior margin semicircular, densely setose in anterior half. Mandibles membranous. Antennae very long; looped, not coiled around apex of abdomen. Anterior and posterior hook plates on abdominal segments 3 and 4, anterior hook plates only on abdominal segments 5 to 8 (Fig. 2E). Abdomen with apical processes present, but not well developed (Fig. 2D). Apex of abdomen with numerous long setae, predominantly ventral. Pupal shelter 15 to 20 mm long, ovoid. Constructed from small fragments of leaves, roots, and other vegetable matter.

HABITAT: Larvae and pupae have been collected from matted roots along the margins of small, fast flowing, forest streams. This in part explains the fact that very few specimens have been collected during stream surveys which have relied upon traditional collecting techniques.

MATERIAL EXAMINED: Victoria—4 pupae, 10 larvae, Cement Creek, Warburton East, 24 Nov. 1981 (Cartwright, Dean); 1 ♀, 1 pharate ♂, 2 pupae, Cement Creek, Warburton East, 8 Dec. 1981 (Cartwright, Dean); 1 larva, Starvation Creek, 10 Mar. 1981 (Cartwright, Dean); 1 larva, Yarra River, O'Shannassy junction, 10 May 1979 (Cartwright, Dean); 1 larva, Buller Creek, Mirimbah, 2 Nov. 1981 (Dean). All specimens in author's collection.

DISCUSSION: Although *pulchripenne* is at present the only Australian species of *Baliomorpha* for which the larva has been described, I have examined unassociated larvae of two other species from eastern Australia. The similarities between the larvae of these three species and *M. variipenne* from central and South America are striking. Features in common include the absence of stridulatory grooves on the ventral surface of the head capsule, the absence of an ecdysial line on the right side

of the anterior ventral apotome, the short, robust mandibles, the absence of antero-lateral brushes on the labrum, the unmodified gena, without a carina, the feather-like gills on abdominal segments 1 to 7, the absence of thoracic gills, and the long slender form of the anal prolegs. In addition pupae of both *B. pulchripenne* and *M. variipenne* possess posterior hook plates on abdominal segments 3 and 4, long looped antennae, and general similarities in the form of the labrum and mandibles. While the suggestion of Flint and Bueno (1982) that species of *Macronema* from North America, Africa and Asia should be transferred to the genus *Macrostemum* is supported by available larval descriptions (Lepneva 1964, Wiggins 1977, Scott 1983), this is certainly not the case with the Australian species. In fact, on the evidence from the larvae, the Australian species and the South American species of *Macronema s. str.* represent a monophyletic unit within the subfamily Macronematinae. Species from the two geographical regions share, for example, the loss of the ecdysial line on the right side of the anterior ventral apotome, which is obviously a derived character. Notwithstanding the similarities detailed above, there are differences between Australian larvae and the larva of *M. variipenne*. Some of these differences are listed in Table 2, and provide supporting evidence for the decision by Neboiss (1984), based on adult morphology, to establish the new genus *Baliomorpha* for Australian species.

Distribution of sister groups in South America and Australia has been reported for several cool-temperate aquatic insect groups, including stoneflies (Illies 1969), chironomid midges (Brundin 1966), and leptophlebiid mayflies (Pescador & Peters 1979). These distributions have been explained in terms of transantarctic dispersal prior to fragmentation of Gondwanaland, and the same dispersal route can satisfactorily explain present distributions of *Macronema* and *Baliomorpha*. This presupposes that ancestral species were cool temperate, and that invasion of tropical regions in South America and Australia/New Guinea has been relatively recent. The great diversification of species in tropical South

IMMATURE *BALIOMORPHA PULCHRIPENNE*

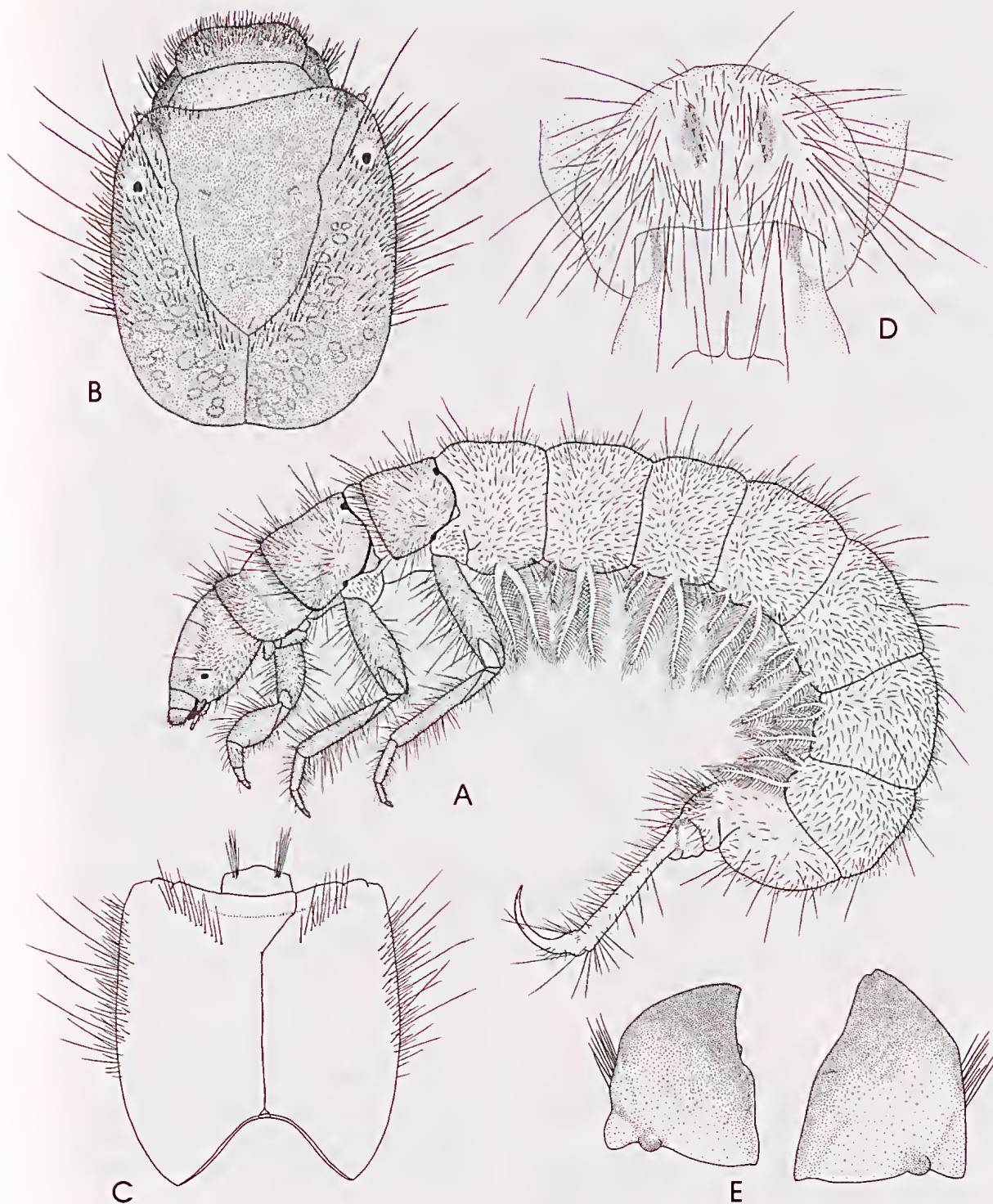


Fig. 1 — *Baliomorpha pulchripenne* (Tillyard), larva. A, whole larva. B, head, dorsal. C, head, ventral. D, ninth abdominal segment and base of prolegs, ventral. E, mandibles.

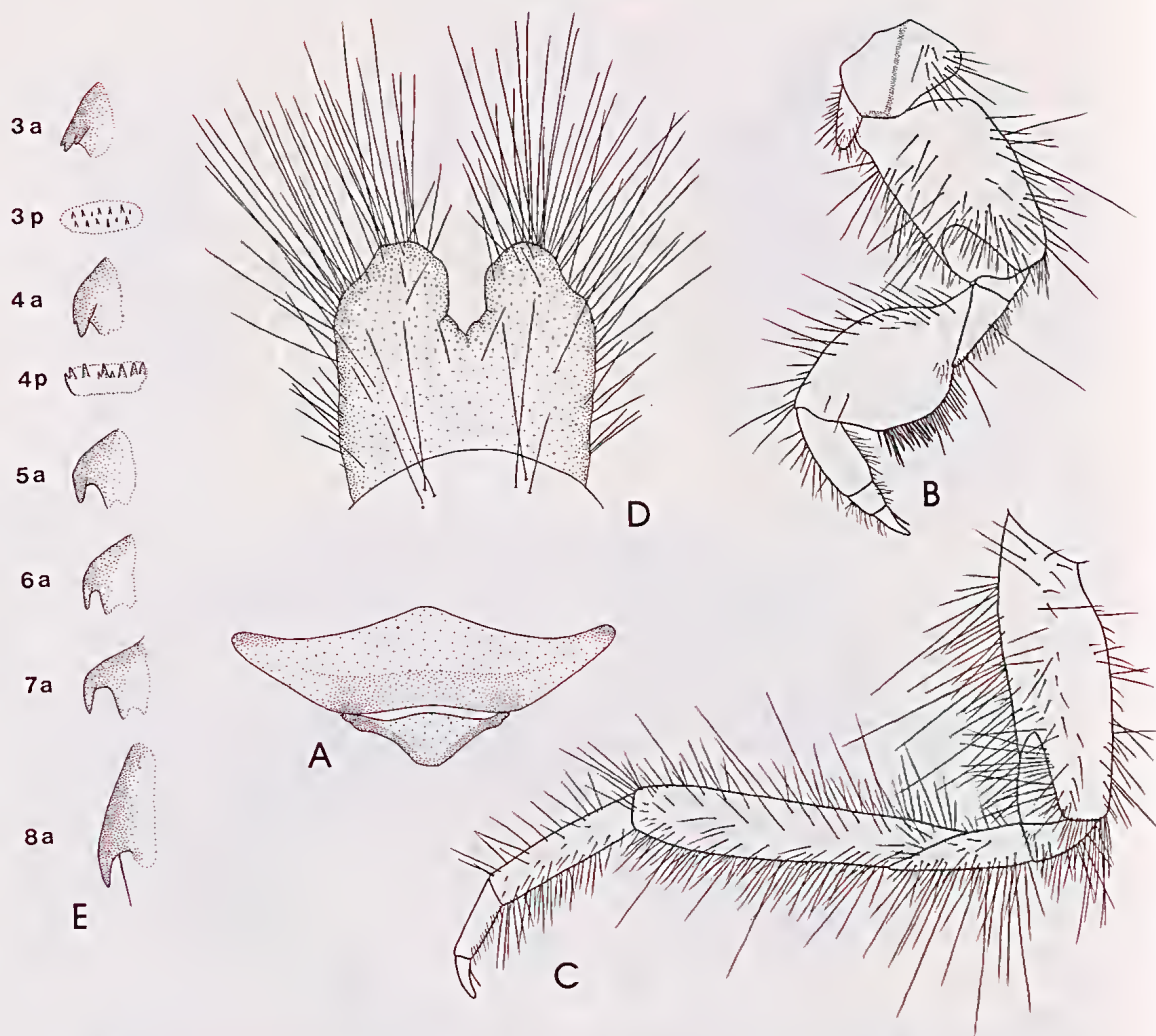


Fig. 2—*Baliomorpha pulchripenne* (Tillyard), larva and pupa. A, larval prosternum. B, larval fore-leg. C, larval mid-leg. D, apex of pupal abdomen, dorsal. E, pupal hook plates, abdominal segments 3 to 8. a, anterior; p, posterior.

America is perhaps a consequence of the suitability of aquatic habitats which support prolific macrophyte growth. Flint and Bueno (1982) have reported that larvae of *M. variipenne* are generally found among the roots and leaves of water plants.

Neboiss (1984) has also recorded a single species of *Macrostemum* from northern Australia, and has drawn attention to the fact that *M. saundersi* (McLachlan) and several other New Guinea species form a natural group, which differs in several adult characters from species of *Macrostemum* in North America, Asia and Africa. While not prepared to formally transfer the New Guinean and Australian species to a new genus, he does recognise that this could ultimately be required. Larvae

of the species from New Guinea and Australia are unknown, which is unfortunate since, as has been shown above, larval stages are particularly useful for clarifying generic relationships. Historically larval morphology has been neglected in Trichoptera systematics, and the inclusion of larvae in future taxonomic studies should be encouraged.

ACKNOWLEDGEMENTS

I wish to thank Dr. Arturs Neboiss for many valuable discussions, and both he and Mr. David Cartwright for critically reading the manuscript.

TABLE 2

DIFFERENCES BETWEEN THE LARVAE OF AUSTRALIAN SPECIES
OF *Baliomorpha* AND *Macronema variipenne*
FROM THE NEOTROPICS

	<i>Baliomorpha</i> Australia	<i>M. variipenne</i> Neotropics (After Flint and Bueno, 1982)
FRONTOCLYPEUS prominent knobs at anterolateral corners	absent	present
FORELEGS femur	broadened	not broadened
ventral setae on femur	simple, robust	palpate
MID- AND HIND LEGS short, peg-like setae on trochanter, femur and tibia	absent	present
apico-dorsal blade-like seta on tarsus	absent	present
ABDOMINAL GILLS formula on segments 5-7	DS, DS, DS	SS, SS, S
ANAL PROLEGS	not jointed in middle	jointed in middle

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A NEW PARACALLIOPIID, *KATOCALLIOPE KUTYERI*
GEN. ET SP. NOV.
(CRUSTACEA: AMPHIPODA) FROM QUEENSLAND

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ABSTRACT: *Katocallope kutyeri* gen. et sp. nov. of the Paracalliopiidae is described from beach sands in Queensland. It exhibits many features characteristic of fossorial amphipods in other families.

Barnard and Karaman established the Paracalliopiidae to accommodate *Paracalliope* Stebbing 1899; and raised *Paracalliope indica* K. H. Barnard 1935 to generic status (*Indocallope*) within that family; the family now embraces 4 species of *Paracalliope* from Australia, New Zealand and Indonesia and one monotypic genus from India (as well as several undescribed Australian species (Barnard & Drummond in preparation)).

Katocallope gen. nov., by virtue of its paired eyes, characteristic male gnathopods and fused second and third urosomites, is deemed to belong in the Paracalliopiidae, and to be distinct from both *Paracalliope* and *Indocallope* at the generic level. Its inclusion necessitates slight amendment to the family diagnosis.

LEGENDS

On figures, capital letters denote morphological parts as follows: A, antenna; B, body; C, coxa; D, dactyl; G, gnathopod; I, inner plate or ramus; L, labium; M, mandible; O, outer plate or ramus; P, pereopod; Q, calceolus; R, uropod; S, maxilliped; T, telson; U, labrum; V, palp; X, maxilla; Y, gill; Z, oostegite.

Lower case letters to the left of the capital letter refer to specimens cited in figure captions; those to the right of capitals or in the body of the drawing are descriptive: d, dorsal; o, opposite; r, right; s, setae removed.

SYSTEMATICS

Family PARACALLIOPIIDAE Barnard & Karaman 1982

DIAGNOSIS: (Additions to the familial diagnosis are italicized.) Head, eyes, coxae 1-3, pereopod 3-6, uropods 1-2 ordinary. Accessory flagellum vestigial *or absent*. Mandibular palp present *or absent*. Coxa 4 poorly excavate posteriorly. Female gnathopods feeble, mittenform *or almost simple*; male gnathopods larger, gnathopod 2 enlarged, wrist small, hand large (usually rotated inward on death), palm oblique. Pereopod 7 elongate, dactyl elongate and setose. Uropods 1-3 extending equally *or not*, peduncle of uropod 3 short to slightly elongate, rami short, equal, lanceolate, outer 1-articulate. Telson laminar, entire. Urosomites 2-3 coalesced.

See Barnard and Karaman (1982) for variables.

Key 1 to the Genera of Paracalliopiidae

1. Palm of male gnathopod 2 with 2 thick spines, mandibular palp absent *Katocallope*
Palm of male gnathopod 2 with 4 thick spines, mandibular palp present 2
2. Inner plate of maxilla 1 with 1 seta *Indocallope*
Inner plate of maxilla 1 with 8+ setae .. *Paracalliope*

Key 2 to the Genera of Paracalliopiidae

1. Inner plates of maxillae 1-2 densely setose medially *Paracalliope*
Inner plates of maxillae 1-2 not setose medially 2
2. Mandibular palp present, peduncle of uropod 3 elongate, epimera with small tooth, palp of maxilliped strongly exceeding outer plate *Indocallope*
Mandibular palp absent, peduncle of uropod 3 short, epimera smooth, palp of maxilliped not exceeding outer plate *Katocallope*

Key 3 to the Genera of Paracalliopiidae

1. Mandible lacking palp, peduncle of uropod 3 short, palp of maxilliped not exceeding outer plate *Katocallope*
Mandible with long palp, peduncle of uropod 3 elongate, palp of maxilliped strongly exceeding outer plate 2
2. Medial margins of maxillae 1-2 naked .. *Indocallope*
Medial margins of maxillae 1-2 setose .. *Paracalliope*

Katocallope gen. nov.

DIAGNOSIS: Paracalliopiidae lacking mandibular palp; inner plate of maxilla 1 poorly armed (generally with 1 seta only); brood plates unexpanded; epimera rounded (lacking notches or small teeth); peduncle of uropod 3 short.

ETYMOLOGY: The prefix Kato is from the Aboriginal Languages, meaning short. The name is feminine.

TYPE SPECIES: *Katocallope kutyeri* sp. nov.

RELATIONSHIP: *Katocallope* differs from *Paracalliope* and *Indocallope* in the lack of teeth on the epimera, the very short palp of the maxilliped, the short uropod 3 with short peduncle, and the absence of a mandibular palp. Pereopods 3-6 of *Katocallope* are more markedly fossorial than those of the other 2 genera; the articles of these pereopods are thicker and shorter, and much

better armed than those of *Paracalliope* and *Indocalliope*.

In addition, *Paracalliope* differs from *Katocalliope* in the medially setose inner plate of maxilla 1 and the expanded oostegites. The latter have not been described for *Indocalliope*.

The slightly tapering coxa 3 of *Katocalliope* and unshortened outer ramus of uropod 2 cannot be evaluated as generic characters until more species have been described and these differences confirmed.

There may possibly be some generic value in the greatly elongate setae of the anterior coxae on *Katocalliope*.

A few species of *Paracalliope* are known to have a vestigial accessory flagellum, but in others its presence requires confirmation. The mandible of *Katocalliope*, besides lacking a palp, is characterized by greater elongation of the molar and extension of the base of the incisor than seems to be typical of *Paracalliope*; but this character too needs further investigation in some *Paracalliope* species. Articles 2-3 of antenna 1 are short and equal in *Katocalliope* and the facial row of setae on maxilla 2 is poorly developed.

The fossorial character and general facies of *Katocalliope* are distinctive within the Paracalliopiidae and bear strong resemblance to two closely allied families, Oedicerotidae and Exoedicerotidae.

Katocalliope kutyeri sp. nov.

Figs 1-4

ETYMOLOGY: *Kutyeri* comes from an Aboriginal word meaning 'thin': in reference to the extremely thin female gnathopods [noun in apposition].

IDENTIFICATION: This is clearly not *Pherusa australis* Haswell (1880, p. 103, pl. 7, fig. 1) because that species, the type of which has been lost, is shown to have a very spinose uropod 3 with elongate peduncle.

DESCRIPTION OF HOLOTYPE MALE 'k' 1.96 mm: Rostrum of medium size, blunt, lateral cephalic lobes small and subacute. Eyes of medium size, with irregular core of pigment at bases of 10 or more ommatidia.

Antennae turned outwards laterally, somewhat fossorial, of medium length; antenna 1 slightly longer than antenna 2, article 1 large, outer facial formula 2+2; articles 2 and 3 short and equal in length; primary flagellum with 7-8 articles, aesthetasc formula 0-1-1-3-5-6-0-0; accessory flagellum probably represented by weak boss. Antenna 2 sharply twisted outwards, gland cone of medium size, article 4 slightly expanded, moderately setose but setae very strong; article 5 shorter and thinner than 4, clavate, bearing stout setae distally; flagellum short, thick, 5-6 articulate, first 2 articles short and irregularly broadened, each with tympanic calceolus on 'dorsal' margin (situated dorsally after antenna 2 flattened on slide).

Epistome flat anteriorly; upper lip articulate, weakly emarginate below.

Mandibular incisor short, teeth ill-defined; lacinia mobilis on each side spine-like, right scarcely distinguishable from closest raker spine, left stouter,

both minutely toothed apically; rakers 3, left rakers of holotype considerably shorter than right (Fig. 3 ML), presumably abnormal or damaged, normal rakers similar on both sides (as in Fig. 3 nMr), increasing in length away from lacinia mobilis; incisorial body (incisor, lacinia mobilis, rakers) basally much extended, almost pediculate from main mandibular body; molar also elongate, constricted just above base, poorly triturative; palp absent, mandibular body normally supporting palp not developed. Lower lip with strong extended mandibular lobes, inner lobes small and fused together.

Inner plate of maxilla 1 leaf-like, with apical point and one apical seta; outer plate large, with 11 spines, orad spines with large thick and blunt serrations (mopped spines), aborad spines thinner, some apparently without serrations or apically bifid; palp thin, articles 1 and 2 subequal in length, apex of article 2 with 4 thick setae.

Both plates of maxilla 2 setose apically, outer plate broad; inner plate distinctive, slightly geniculate, directed outwards across outer, bearing a straggling row of 5 or 6 setae of different lengths almost submarginally as well as several medial setae and 2 medium-length stiff setae on a sub-basal protruberance covered with a stubble of fine setules.

Maxillipeds large, inner plate broad and apically flat and spinose; outer plate enlarged, dwarfing palp, with one strong apical seta, medial margin with spatulate spines and aboral pairs of facial spines; palp relatively small, scarcely exceeding outer plate, dactyl unguiform, with 2 accessory apical setules.

Coxa 1 expanded distally, coxae 2-3 tapering distally, coxa 4 adz-shaped and weakly bevelled ventrally, not as enlarged, relatively, as in female; coxa 5 scarcely shorter than 4; long ventral setae of coxae 1-3, 8-1-1; of coxa 4 in two groups of 5 and 1; short ventral setae on coxa 1, 1 anterior, 2 posterior; coxae 2-4, 1-1-1.

Gnathopod 1 small, wrist of medium length, lobate, hand slightly longer than wrist, expanded palm naked, very oblique and poorly defined but with small callus at posteroproximal limit and 4 facial setae on hand close to margin; dactyl not reaching apex of palm when closed.

Gnathopod 2 large, wrist of medium length, lobate, lobe narrow and pointing slightly distad; hand much longer than wrist, expanded, palm oblique and deeply excavated in middle, this sinus bearing 2 thick spines, proximal limit of palm with large callus delimited by row of setae; dactyl not reaching apex of palm when closed, resting in shallow depression about middle of callus.

Pereopods 3-4 typically fossorial with article 4 elongate and some articles bearing very thick stiff setae; dactyls without visible slits but with absorbed nail and external apical flake.

Pereopods 5-6 short, fossorial as in Oedicerotidae, with strongly setose articles 4-5.

Pereopod 7 greatly elongate as in Oedicerotidae and other Paracalliopiidae, articles 5 and 6 slightly more spinose anteriorly than in *Paracalliope*; dactyl (article 7) typically elongate and setose.

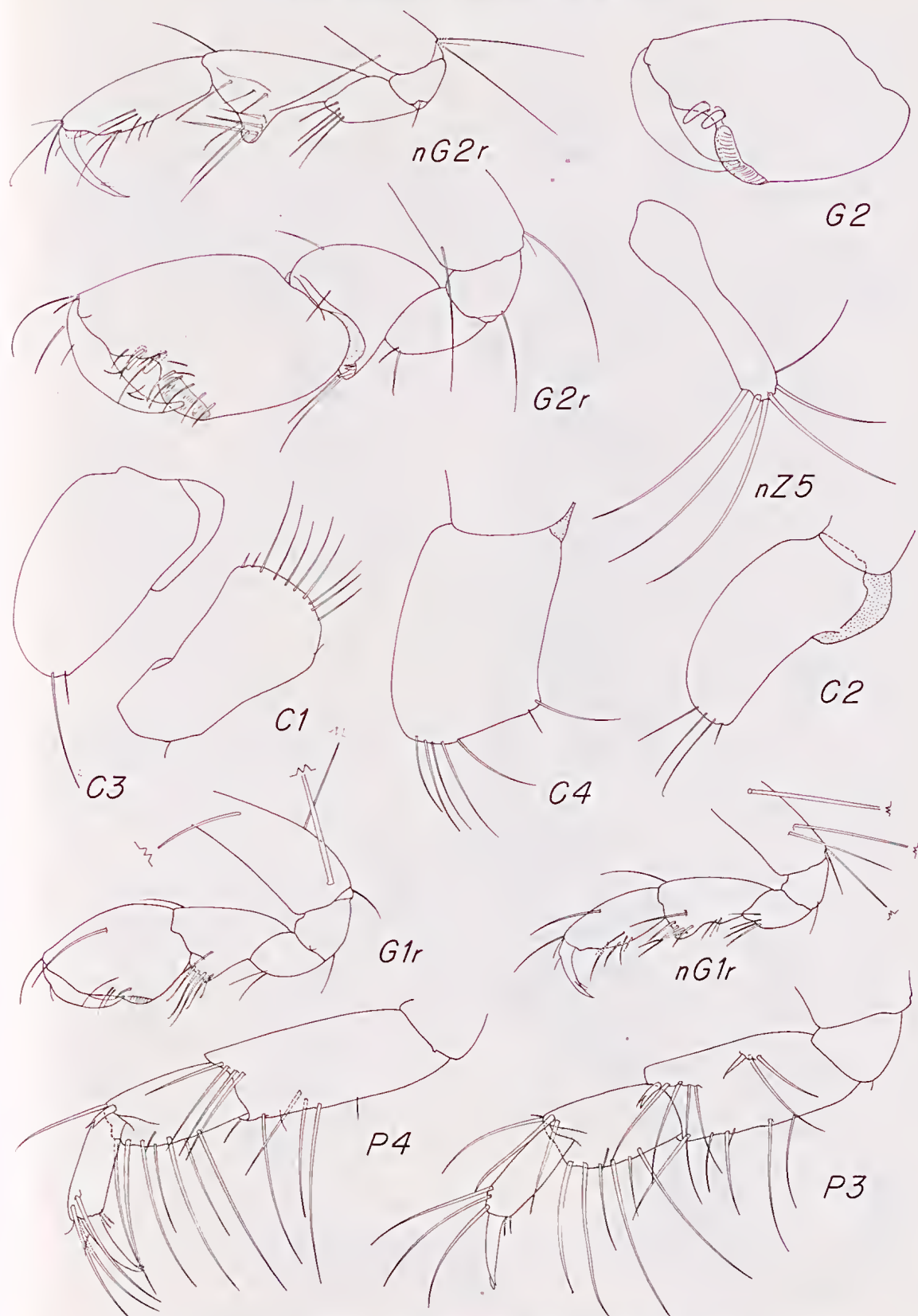


Fig. 1—*Katocallope kutyeri*, unattributed figures, male holotype 'k'; n, female 'n'.

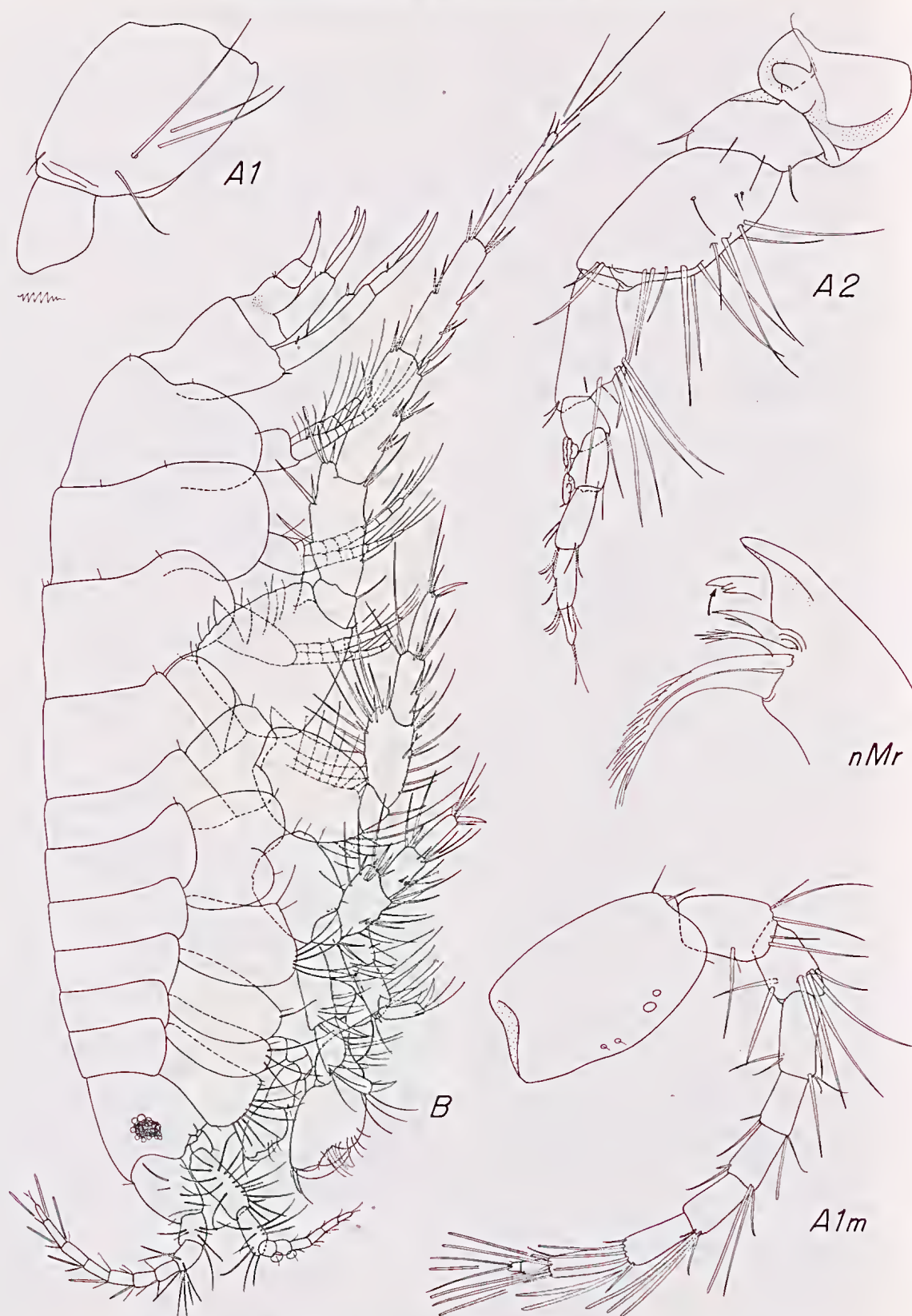


Fig. 2—*Katocallope kutyeri*, unattributed figures, male holotype 'k'; n, female 'n'.

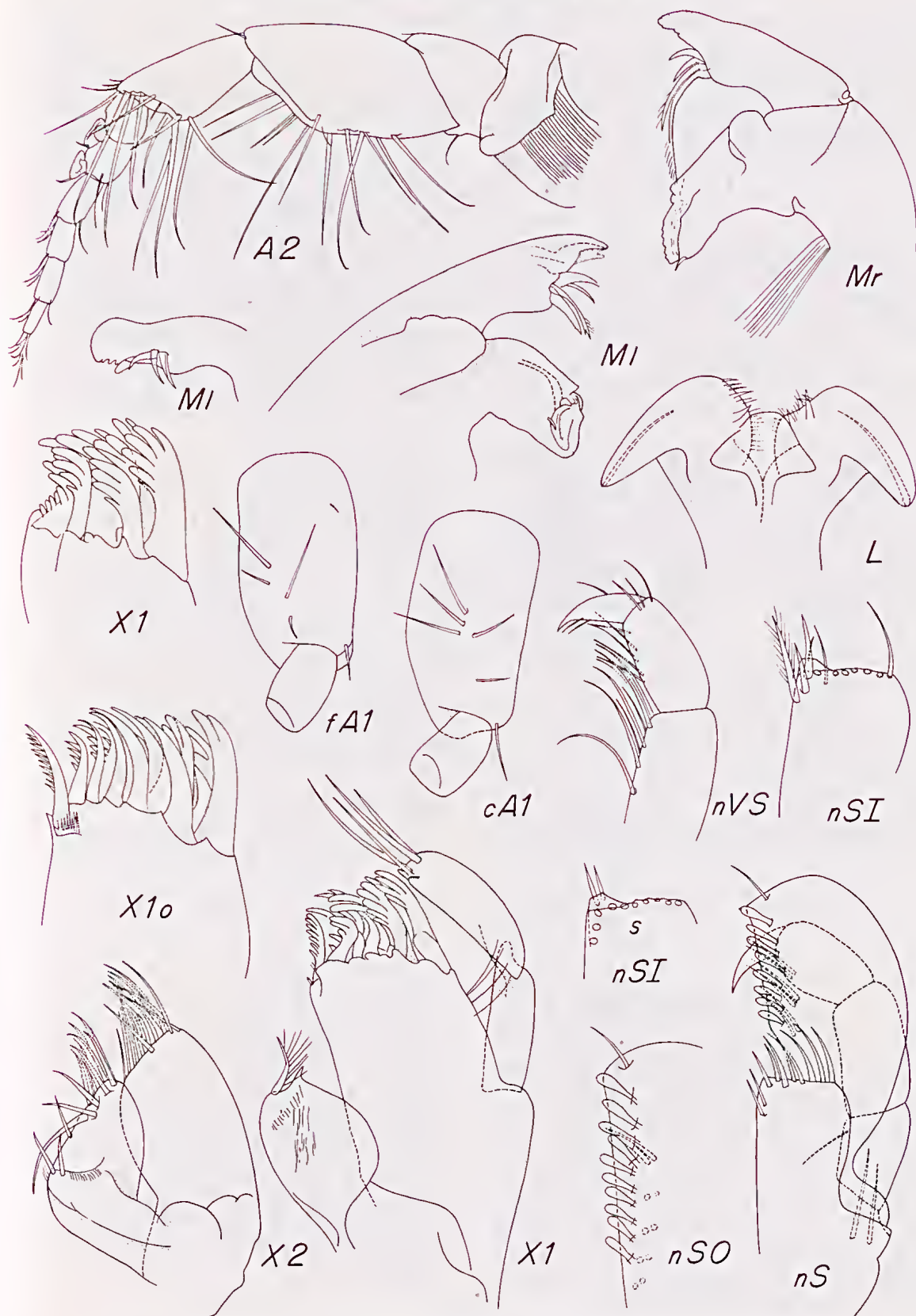


Fig. 3—*Katocalliope kutyeri*, unattributed figures, male holotype 'k'; c, female 'c'; f, female 'f'; n, female 'n'.

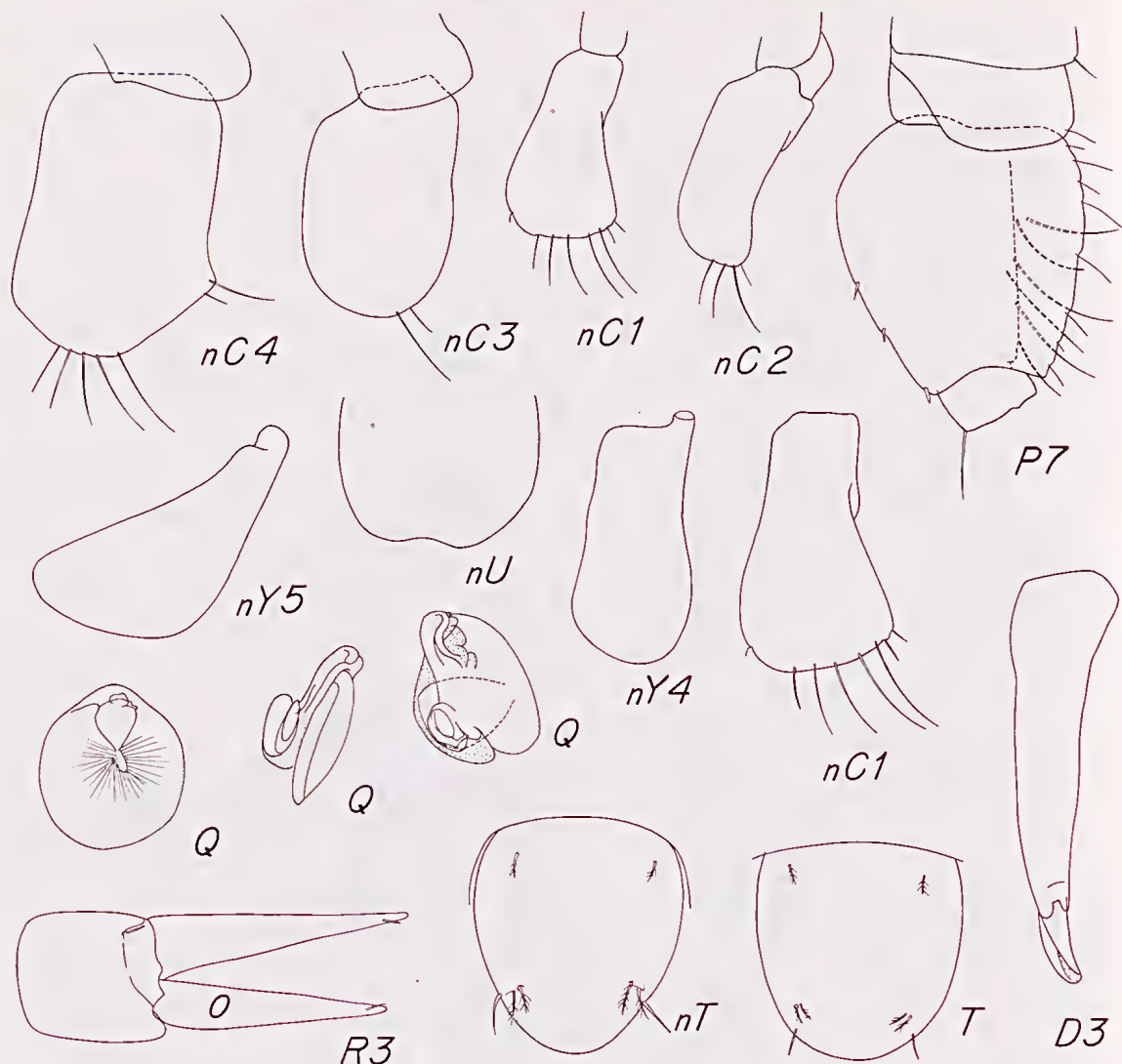


Fig. 4—*Katocalloipe kutyeri*, unattributed figures, male holotype 'k'; n, female 'n'.

Gills present on coxae 2-6, rectangular or clavate.

Pleopods ordinary, peduncles elongate, rami elongate, subequal and multiarticulate. Pleonal epimeron 2 dominant; all epimera rounded posteroventrally. Urosomites 2-3 fused together. When urosome unflexed uropod 1 extending beyond uropod 2, and both beyond uropod 3; all naked except outer ramus of uropod 1 with 1 spine; peduncle of uropod 1 with inner spine and outer setule, dorsal base of outer edge with 1 spine; peduncle of uropod 2 with strong spine on each apex. Peduncle of uropod 3 short, inner ramus weakly dominant, each ramus lanceolate, with subapical setule, otherwise naked. Telson short, ovate, entire, dorsally with pair of basolateral setules, 2 pairs of apicolateral setules, each apicolateral margin with setule.

FEMALE 'n': Like male but calceoli absent and aesthetascs fewer (one aesthetasc each only on last 2 articles of antenna 1); flagellum of antenna 1 with only 6 articles, first 2 flagellar articles of antenna 2 unthickened. Gnathopods 1-2 both very slender, hands and wrists subequally long, wrists lobate, lobe on gnathopod 2 pointing posteriorly and not distally as in most species of *Paracalliope*; palms obsolescent, oblique, poorly defined by setal groups; dactyls thin, curved, each with 2 subapical accessory setules.

Coxae 1-4 relatively more diverse than in male, coxae 2-3 tapering less, coxa 4 much larger than coxae 1-2, broader than in male, with broadened anteroventral region.

Oostegites present on coxae 2-5, narrow, apically setose.

VARIATIONS: The number of flagellar articles on antenna 1 varies from 6-8 in males (apparently mature) and from 5-6 in females with setose oostegites; on antenna 2 between 5 and 6 in males and usually 5 in females. Setal formula on the outer face of antenna 1 is usually 3-2 in larger specimens (near 2 mm) and 2-2 in smaller specimens (near 1.75 mm). The number of calceoli on male antenna 2 is always 2. Visible ommatidia vary from 5-10 in adults. Coxae 1-3 vary more than most other features in this species because of the strong sexual distinctions; and the numbers of setae on each varies slightly between individuals, even of approximately the same size. Lateral facial armature formulas on article 4 of pereopods 3 and 4 are also variable: the formula for pereopod 3 on female 'e' is 6-2; female 'f', 4-2; female 'n', 4-1; male 'z', 4-2; formula for pereopod 4, female 'c', 5-0; female 'f', 4-0; female 'n', 4-0; male 'z', 3-0 with no spine present.

Uropods are very consistent (though occasional rami have an aberrant setule or rudimentary spine) in that only the outer ramus of uropod 1 is armed; it carries a thick sub-basal spine. The peduncle of uropod 1 has a dorsobasal spine, an apicolateral setule and an apicomedial spine. The peduncle of uropod 2 carries a thick spine apically on each side.

ILLUSTRATIONS: To show relative size differences of coxae in the two sexes drawings of male and female coxa 4 have been adjusted to the same size and coxae 1-3 drawn to the magnification appropriate for each sex. In the female (which is the 'basic' expression of the species) coxa 4 is much larger than coxa 1; but in the male this disparity is reduced during development, and in the adult coxa 4 has become smaller, relative to coxa 1, than it is in the female.

The short second and third mandibular raker spines of the holotype (illustrated) are not the normal condition in this species. Examination of 10 other specimens

shows rakers to be similar on both sides. Serrations on the first raker, usually rather obscure, are not shown.

Maxilla 2 is abnormally flattened and the outer plate skewed in order to represent setae in their full length. In normal aspect the plates are more closely attached at the base, and the basomedial setae less sub-marginal.

Lateral setae on palp article 3 of the maxilliped are not shown in illustrations.

HOLOTYPE: Museum of Victoria J6931, male 'k' 1.96 mm.

TYPE LOCALITY: Redcliffe Beach near Brisbane 27°14'S, 150°07'E, coll. Deborah M. Dexter, 15 April 1981, core taken at low tide between tide lines. Voucher Material: Type locality, J6935 female 'c' 1.99 mm, J6934 female 'f' 1.80 mm, J6932 female 'n' 1.90 mm, J6933 female 'r' 1.78 mm, J6936 male 'z' 1.67 mm + 8 slides.

OTHER MATERIAL: 60 specimens all from type locality.

DISTRIBUTION: Known only from type locality.

ACKNOWLEDGEMENTS

Our material was collected by Dr. Deborah M. Dexter, San Diego State University, California and we are most grateful to her for making it available to us.

We thank Caroline Cox Lyons of New York City for inking our plates; and at Smithsonian Institution Jan Clark and Patricia B. Crowe for laboratory assistance.

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A NEW LIZARD OF THE GENUS *AMPHIBOLURUS* (AGAMIDAE) FROM SOUTHERN AUSTRALIA

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ABSTRACT: A new species of the genus *Amphibolurus* is described from the mallee heath belt of north-western Victoria, eastern South Australia and the Eyre Peninsula. Its relationships with its congeners and the closely related *Cainanops* are discussed. Morphometric data for these species are presented.

During research in both the Big and Little Desert mallee country of western Victoria, lizards closely resembling *Amphibolurus nuiricatus* were collected. Examination of specimens from this population and museum specimens from the South Australian Museum revealed the presence of two species, one of which has not previously been described. Material is housed in the Museum of Victoria (prefix D) or the South Australian Museum (prefix R).

SYSTEMATICS

Amphibolurus norrisi sp. nov.

Figs 1, 2

1978 *Amphibolurus nuiricatus* (part) Houston, p. 38.

HOLOTYPE: D51499, an adult male from 29 km S of Nhill in 36°36'S, 141°38'E, collected by A. J. Coventry and K. C. Norris, 5 Oct. 1978.

PARATYPES: There is a total of 40 paratypes, 20 males, 15 females and 5 juveniles. All are from the Little Desert in the Victorian Wimmera. D8944, Kiata; D14799, Broughtons Waterhole; D14800-1, 3.2 km NE of Broughtons Waterhole; D14802-3, D14810, Stans Camp, approx. 22.5 km SW of Nhill; D14804, D14809, 1.6 km E of Broughtons Waterhole; D14808, 10.5 km E of Broughtons Waterhole; D14805-7, D14813, 1.6 km ESE of Broughtons Waterhole; D14811, Kiata Lowan Sanctuary; D14812, 4 km W of Broughtons Waterhole; D33526-7, Little Desert; D51482, D51500, 12 km S of Winiam; D51491, 33 km S of Nhill; D51507, 3 km S of Broughtons Waterhole; D51512, 10 km S of Winiam; D51521, 35 km S of Nhill; D51576, 8 km SSW of Kiata; D51597, D51626, 24 km S of Kiata; D51608, D51771-2, Salt Lake, 18 km S of Kiata; D51617, 25.5 km S of Kiata; D51752, 18 km NE of Gorokey; D51759, 10 km SW of Kinimakatka; D51763, 15 km SW of Kinimakatka; D51764, 15 km NE of Gorokey; D51765-6, Chinamans Flat, 5 km E of Broughtons Waterhole; D51783, 23 km S of Kiata; D51786, 8 km SE of Winiam; D52230, 25 km SW of Kaniva.

DIAGNOSIS: Lateral scales at least moderately heterogeneous, usually with a mid-lateral row of enlarged mucronate scales. Dark line running along the canthus rostralis from tip of snout to orbit. Dorsum of snout with or without a median dark stripe extending

forward from between the orbits, no transverse dark marks on snout.

DESCRIPTION: Relatively large agamid lizard with limbs and tail of moderate length in adults, but short in hatchlings. Somewhat elongate in form. Very similar in scutellation to *A. nuiricatus*, differing in having a less prominent nuchal crest and vertebral scale ridge. Two dorsal rows of enlarged mucronate scales on either side, and usually a third on the lateral aspect of the body. Both dorsal and lateral scales strongly heterogeneous in adult. Dorsal scales in rows parallel to, or weakly convergent upon, midline. Gular scales feebly keeled to smooth. Pre-nasal scales 4-6, subnostril scales 3-5, supralabials 13-17, infralabials 10-15, mid-body scale rows 84-106, lamellae under fourth toe 24-28. Preanal pores 4-11 ($m=6.4$, $n=117$), femoral pores 4-8 ($m=5.6$, $n=117$), on posteroinferior aspect of thigh.

General colour from slate grey to brown patterned with dark grey to black markings. Sides below dorsolateral skin fold darker. Broad median dark stripe, with or without transverse connections to the dark lateral area forming a series of lozenge-shaped lighter areas. Tail with obscure dark blotches at base, becoming progressively more distinct and forming bands on the distal half of the tail. Temporal and occipital regions with fine dark reticulations. Dark stripe from eye to tympanum, bordered above with a narrow paler stripe. Lower labials very pale to white. Upper and lower lips pale, the pale area extending posteriorly onto jowls (Fig. 1), this latter area occasionally tinged orange. Lining of mouth pale yellow.

DESCRIPTION OF HOLOTYPE: Snout-vent (SVL) length 69 mm, tail 143 mm, femoral pores 4 (2 on each side), preanal pores 7 (4 on right, 3 on left). Dorsal scales weakly convergent on midline, gular scales very feebly keeled. Prenasal scales 5, subnostril scales 5, supralabial scales 15, infralabial scales 15, mid-body scale rows 104.

DISTRIBUTION: Mallee heath belt of northwestern Victoria, extending westward into South Australia. A separate population on Eyre Peninsula, extending onto the coast of the Great Australian Bight (Fig. 2).

ETYMOLOGY: This species is named in honour of Kenneth Charles Norris, formerly of the Victorian Fisheries and Wildlife Department Survey Team, in recognition



Fig. 1—*A. norrisi* from Chinaman Well area, Big Desert.

of his contributions to the knowledge of the Victorian vertebrate fauna.

OTHER SPECIMENS EXAMINED:

Victorian localities—D51668, D51729, 18 km W of Ranger's Office, Wyperfeld National Park; D52550, D52654, D52696, D53010, D53072, D53854, D54154, D54202, D55004, 0.2 km NE of Chinaman Well; D52557, D52677, D53069, D54793, D55458, 2 km NNW of Chinaman Well; D52562, D53501, D54095, D54119, 2.8 km NE of Chinaman Well; D52632, D52687, D53051, D54028, D54127, D54150-2, D54942, D54976, 2.75 km NNW of Chinaman Well; D52678, 4.7 km ENE of Chinaman Well; D52693, 6.6 km ENE of Chinaman Well; D52751, 2 km S of White Springs (i.e. 21 km S of Tutye); D52758, 22 km S of Tutye; D52996, D53470, D54027, D54124, D54755, D54966, 3.3 km NNW of Chinaman Well; D53057, D53077, D53965, D56740, 5.1 km NNW of Chinaman Well; D53465, D53916, D54143, D54646, 6.2 km ENE of Chinaman Well, D53466, D53855, 3 km NE of Chinaman Well, D53488, 2.2 km NNE of Chinaman Well; D54094, 16.6 km ENE of Chinaman Well; D54794, 1.7 km NNW of Chinaman Well; D54928, D54935, 2.65 km SE of Chinaman Well; D54967, 1.3 km N of Chinaman Well; D54968, 2.25 km NW of Chinaman Well; D54977, 4.4 km NNW of Chinaman Well; D55035,

2.7 km NNW of Chinaman Well; D55267, 5.7 km NNW of Chinaman Well; D55606, 1.3 km N of Chinaman Well; R10880, Moonlight Tank.

South Australian localities—R1454, Tintinara; R2359 A-B, Coombe; R3269 A-C, 'Euringa', Naracoorte; R4304, 24 km N of Fowlers Bay; R9006, County Chandos; R10134, R10138, R13550, Hineks National Park; R10177, Hund. of Blessing; R13355, Bookmark Station; R13549, 18 km ESE of Halidon; R13926, sec 17, Hund. of Jamieson, Eyre Peninsula; R14197, N/R Minaro Downs Station, between Poldia and Wudinna; R16057, Lincoln National Park; R16171, about 47 km S of Lameroo, 11 km W of Verran Hill, Hineks National Park; R16681, Billiat Conservation Park, 34° 55'S, 140° 20'E; R21446, R21472, Naracoorte, about 36° 40'S, 140° 00'E; within 5 km Wirrildee Station; R21951, Naracoorte, about 36° 40'S, 139° 59'E; Wirrildee, about 25 km E of Kingston; R23783, Lincoln, 34° 51'S, 135° 57'E; Lincoln National Park.

DISCUSSION: *Amphibolurus norrisi* is in some respects intermediate between *A. muricatus* (White 1790) and *A. nobbi coggeri* Witten 1972. It is very similar to the former in scutellation, but in colour pattern and ecology appears to more closely resemble *A. nobbi coggeri*. In the eastern part of its range it occurs to the north of the distribution of *A. muricatus*. *A. nobbi coggeri* and *A.*

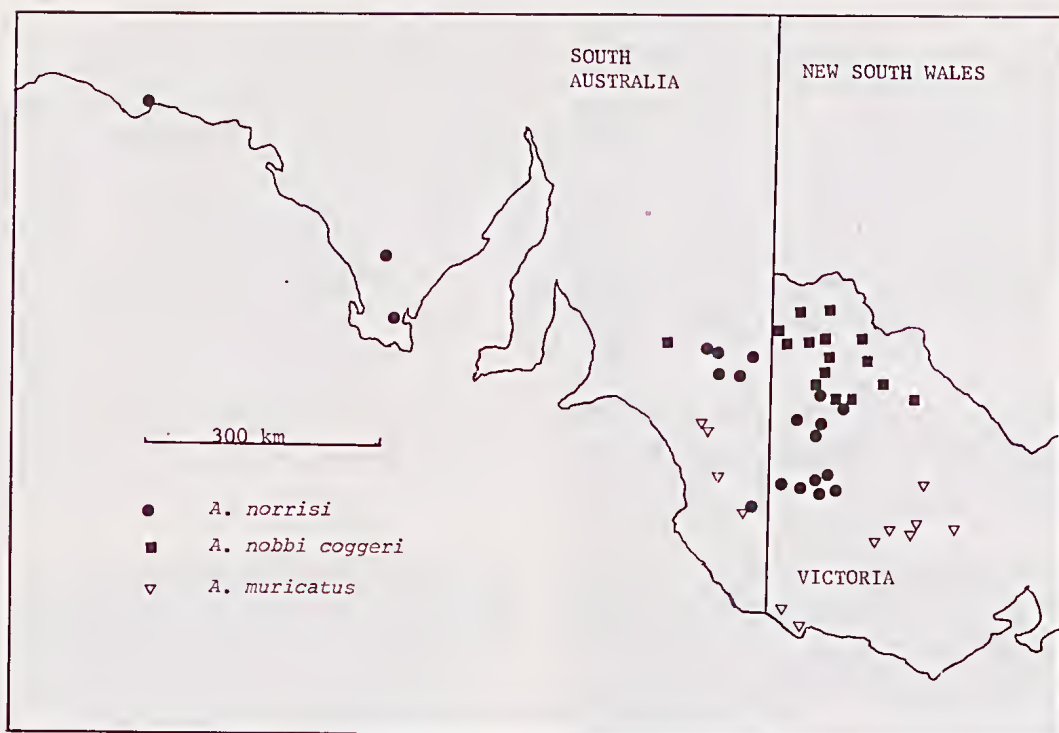


Fig. 2—Map showing distribution of *A. norrisi*, with *A. muricatus* and *A. nobbi coggeri* from adjacent areas.

norrisi are sympatric in the northern part of the range of *A. norrisi* east of Spencer's Gulf (Fig. 2). Mather (1979) and Menkhorst (1982) reported this sympatry in the Victorian part of the range (reporting *A. norrisi* as *A. muricatus*), and the area of sympatry probably extends into South Australia (Houston 1978).

A. norrisi and *A. muricatus* are readily distinguishable from *A. nobbi* by their more heterogeneous dorsal and lateral scalation. *A. norrisi* differs most strikingly from *A. muricatus* in colour pattern. The most consistent difference is the presence of a dark canthal stripe in *A. norrisi*. Rare specimens of *A. muricatus* have a dark canthal stripe from the tip of the snout to the nostril, but this stripe does not continue back to the orbit as it consistently does in *A. norrisi*. Also, *A. muricatus* often possess transverse dark markings on the snout, running between the nostrils. Such markings are never present in *A. norrisi*, where the only dark dorsal snout marking is a median longitudinal stripe. This median stripe may extend as far anteriorly as the level of the nostrils, but does not extend to the snout tip.

A. norrisi has generally more scales than other *Amphibolurus* (Table 1). In this it resembles *Caimanops*. However, *A. norrisi* has small scales in the loreal region, with a generally higher number of prenostril and subnostril scales than other *Amphibolurus* and *Caimanops* (Table 1). *A. norrisi* is also distinct from other taxa in this group by virtue of its relatively smooth gular scales.

The recorded number of supralabial scales in most agamids is subject to wide variation. Often the supralabial series of elongate scales continues posteriorly beyond the lip, and these posterior scales *sensu stricto* are not supralabials. Various authors have chosen to count only scales on the upper lip, the whole series, or only those scales anterior to the tendon of *levator labii inferioris*, the effective angle of the mouth. The number of infralabial scales is not so prone to observer variation, and should be preferred in taxonomic work on agamids (Witten 1982).

The number of pores is higher in *A. norrisi* than in other *Amphibolurus* (Table 1). *A. norrisi* most commonly has 6 preanal and 6 femoral pores. *A. nobbi* typically has 6 preanal and 4 femoral pores, whereas *A. muricatus* has 6 femoral and 4 preanal pores (Witten 1972a).

A. norrisi appears to be more elongate than both *A. muricatus* and *A. nobbi*. This appearance is certainly enhanced by differences in colour pattern. A preliminary morphometric analysis reveals little variation between three species of *Amphibolurus* (Table 2). *A. norrisi*, however, has a narrower head than other *Amphibolurus*, which is consistent with a more elongate form. *A. norrisi* has a slightly narrower tympanum, and the forelimb and thigh measurements are less than for other *Amphibolurus*. In these measurements *A. norrisi* deviates from other *Amphibolurus* in the same direction as *Caimanops* (Table 2). In each case *Caimanops* is

TABLE 1
COMPARATIVE SCALE COUNTS FOR *Amphibolurus* AND *Caimanops*†

	<i>A. norrisi</i>		<i>A. muricatus</i>		<i>A. nobbi</i>		<i>C. amphiboluroides</i>	
	Range	Mean \pm SD(N)	Range	Mean \pm SD(N)	Range	Mean \pm SD(N)	Range	Mean \pm SD(N)
PNS	4-6	4.89 \pm 0.7(19)	3-5	3.58 \pm 0.7(12)	3-5	3.62 \pm 0.6(16)	3-5	4.09 \pm 0.6(23)
SNS	3-5	4.37 \pm 0.8(19)	3-4	3.42 \pm 0.5(12)	2-4	3.19 \pm 0.5(16)	2-5	3.00 \pm 0.7(23)
INS	9-13	11.6 \pm 1.1(17)	9-13	11.5 \pm 1.4(12)	11-13	11.4 \pm 0.6(16)	5-9	6.78 \pm 0.9(23)
SLS*	10-14	12.7 \pm 1.2(19)	10-14	11.8 \pm 1.1(12)	8-11	10.0 \pm 1.0(16)	11-15	12.8 \pm 1.2(23)
ILS	10-15	12.9 \pm 1.3(19)	9-13	11.2 \pm 0.9(12)	9-11	10.0 \pm 0.7(16)	11-14	12.3 \pm 1.1(23)
MBS	84-106	98.7 \pm 7.1(16)	72-97	87.3 \pm 6.8(11)	64-75	68.7 \pm 3.2(16)	93-131	107 \pm 9.9(20)
PP	4-11	6.44 \pm 1.2(117)	3-6	4.08 \pm 0.8(12)	4-6	5.44 \pm 0.9(16)	2-6	3.81 \pm 1.1(21)
FP	4-8	5.63 \pm 1.0(117)	4-7	5.83 \pm 1.1(12)	2-4	2.75 \pm 0.9(16)	0-2	0.09 \pm 0.4(21)

PNS=Prenostrils; SNS=Subnostrils; INS=Internostrils; SLS=Supralabials; ILS=Infralabials; MBS=Mid-body scales; PP=Preanal pores; FP=Femoral pores.

* Supralabials counted following the methods of Witten (1982), counting only scales anterior of the tendon of levator labii inferioris.

† Data for species other than *A. norrisi* from Witten (1982).

much further from *Amphibolurus* than is *A. norrisi*, and we do not consider the generic status of *Caimanops* needs to be questioned at this stage. However, as *A. norrisi* also resembles *Caimanops amphiboluroides* in colour pattern and in several scale characters it seems very likely that *A. norrisi* is more closely related to *Caimanops* than are the other species of *Amphibolurus*. This apparent relationship indicates that the nearest relatives to *Caimanops* are in *Amphibolurus* and not *Diporiphora*, the genus to which it was originally referred.

It appears that Houston (1978) has based much of his description of *A. muricatus* on *A. norrisi*. His description of 'ventral scales flat and virtually smooth, feebly keeled on chest' is not descriptive of typical *A. muricatus*. The colour description of 'upper and lower lips usually whitish' also appears to relate to *A. norrisi*. The pore arrangement in '*A. muricatus*' (Houston 1978,

fig. 4G) shows a specimen with 8 preanal and 6 femoral pores, a condition well within the normal range for *A. norrisi* but unusually high for *A. muricatus*.

The Eyre Peninsula population of *A. norrisi* appears to attain greater size than the population in eastern South Australia and Victoria. The largest Eyre Peninsula specimen is a female of 117 mm snout-vent length (R13926). The largest Victorian specimen is also a female of 104 mm SVL (D53488). Generally *A. norrisi* females tend to attain larger sizes than males, as is the case in *A. nobbi* (Witten 1972a). However, the largest *A. muricatus* examined were males.

Ovaries of *A. norrisi* begin to enlarge very late in winter. By early September females have oviducal eggs, and gravid females were not collected after late November. The number of eggs ranges from 3 to 7, with a mean of 4.82 (N=17). Three females examined in late November had slightly enlarged ovaries, and convoluted

TABLE 2
MORPHOMETRIC DATA FOR *Amphibolurus* AND *Caimanops*

	<i>A. norrisi</i> (N=36)			<i>A. muricatus</i> (57)			<i>A. n. nobbi</i> (19)			<i>C. amphiboluroides</i> (22)		
	a	X30	X80	a	X30	X80	a	X30	X80	a	X30	X80
Tail length	1.177	51.7	164	1.161	55.9	175	1.344	53.9	201	0.964	50.9	131
Hind Limb	0.988	21.8	57.4	0.958	23.7	60.5	1.101	21.7	63.9	1.016	16.2	44.0
Pes Length	0.902	10.2	24.8	0.877	11.4	27.0	1.050	10.2	28.6	0.963	7.0	18.1
Thigh	1.012	16.5	44.4	1.017	17.1	46.3	1.114	15.9	47.4	1.019	13.9	37.8
Fore Limb	0.921	12.5	30.9	0.945	12.8	32.2	0.979	12.8	33.4	0.956	11.8	30.1
Snout-parietal	0.773	8.00	17.1	0.773	7.99	17.1	0.752	7.71	16.1	0.833	6.69	15.1
Head Width*	1.025	7.64	16.9	1.106	7.43	17.5	1.084	7.53	17.4	0.951	7.45	15.5
Snout-ear*	1.147	8.74	21.2	1.160	8.56	21.0	1.196	8.51	21.4	1.123	9.01	21.4
Head Depth*	1.042	5.25	11.7	1.102	5.02	11.8	1.029	5.33	11.8	1.203	4.75	12.0
Ear Width*	1.241	1.33	3.46	1.308	1.31	3.61	1.370	1.47	4.25	1.079	1.44	3.31

a=allometric coefficient from the equation $x=ky^*$, where x =length of part, k =a constant, y =snout-vent length.

X30=length of part in mm calculated at snout-vent length of 30 mm.

X80=similar figure for s-v of 80 mm.

Thigh measurement from knee to knee with thighs perpendicular to body axis.

* regressed against snout-parietal interval.

oviducts, as did those examined in December. Females examined in January and March did not have enlarged ovaries, indicating that there is no autumn clutch of eggs as in *A. nobbi* (Witten 1972b). Hatchlings first begin to emerge in January. The smallest recorded hatchling had a SVL of 31.5 mm (recorded in February). Maturity is not attained until at least the beginning of the second breeding season (Table 3).

TABLE 3
MEAN SIZE OF IMMATURE *A. norrisi*

Month	Mean SVL	N
January	33.0	1
February	34.7	3
March	40.3 (34.7-46.7)	9
October	43.5	3
November	56.7	3

A. norrisi preys primarily on small arthropods, but the presence of one vertebrate prey item (a skink) suggests that it may be an opportunistic feeder. Table 4 lists food items found in the stomachs of *A. norrisi*.

TABLE 4
STOMACH CONTENTS FROM *A. norrisi* (N=51).

Prey Item	Present in
Hymenoptera	
Formicoidea	66.7 (34)
Apoidea	3.9 (2)
Apocrita (Excluding above)	3.9 (2)
Coleoptera	
Scarabaeidae	58.8 (30)
Curculionidae	25.5 (13)
Lepidoptera	35.3 (18)
Hemiptera	29.4 (15)
Orthoptera	17.6 (9)
Arachnida	13.7 (7)
Blattodea	9.8 (5)
Diptera	3.9 (2)
Scincidae	2.0 (1)

'Present In' refers to the percentage of specimens in which the prey item was found, with the actual number in parentheses.

ACKNOWLEDGEMENTS

The authors wish to thank the following people: Dr. T. D. Schwaner, South Australian Museum, for the loan of specimens in his care; Miss E. M. Matheson, Museum of Victoria, for identification of stomach contents; Fisheries and Wildlife Department Survey Team members, and Mr. P. A. Rawlinson and students, La Trobe University, for assistance in obtaining specimens; Fisheries and Wildlife Department for collecting permits to the Museum of Victoria. Special thanks go to Mr. P. Robertson, Melbourne University for his help, encouragement and companionship during many field trips with A.J.C.

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ZOOPLANKTON ABUNDANCES IN BASS STRAIT AND WESTERN VICTORIAN SHELF WATERS, MARCH 1983

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ABSTRACT: Three sets of zooplankton samples taken during a cruise to central Bass Strait and on a transect from central Bass Strait to Portland, Victoria have been analysed. Bass Strait holozooplankton consisted of few species, with salps, larvaceans, cladocerans, euphausiids and the copepods *Calanus australis*, *Paracalanus indicus* and *Oithona* spp. most abundant. Zooplankton of the western Victorian shelf resembled that of the Bass Strait neritic zone.

Little is known of the zooplankton of Bass Strait or of the Victorian continental shelf. Dall (1957, 1958) briefly described the distribution of crustacean zooplankton, mainly copepods, and identified several distinct water masses on the basis of zooplankton species composition. Noone (1979) described the composition of zooplankton in a series of summer cruises throughout the Strait. Watson and Chaloupka (1983) presented a species list for the Strait on the basis of four cruises; they listed 85 species of copepods and 39 other holoplankton species from their samples. Abundance data from that study, and from a more recent study of neritic zooplankton in Bass Strait, are in preparation (G. F. Watson, pers. comm.).

We report here a study of zooplankton taken on Cruise 83-K-2 of HMAS *Kimbla*. Three series of zooplankton samples were collected: twelve horizontal tows near a drogue; sixteen stratified tows for depth profiles; and 70 pump samples taken along a transect from central Bass Strait to Portland, Victoria. The aim of this study was to provide data on small-scale variability in plankton abundances within Bass Strait, to complement the larger-scale studies described above. Data on phytoplankton productivity and zooplankton growth rates taken during this cruise will be presented elsewhere (R. A. Congdon and W. J. Kimmerer, unpub. data).

METHODS

A drogue was launched at 0800 on 9 March 1983 at 39°29.5'S, 144°58.6'E (Fig. 1). The drogue consisted of a 9 m parachute attached to a weighted wire suspended 30 m below a surface float. Zooplankton samples were taken near the drogue until 1925 hours on 13 March, when the transect was started. Throughout the cruise temperature profiles were taken with expendable bathythermograph (XBT) drops, and surface temperature was recorded from a temperature gauge on the ship.

Zooplankton samples at the drogue were taken twice daily using a 0.5 m mouth, 100 μ m mesh conical net towed horizontally at 30 m depth. We collected stratified samples by duplicate horizontal tows with 30 cm mouth, 190 μ m mesh Clarke-Bumpus nets at 0, 15, 30 and 50 m depth; one set of samples was collected around noon on 12 March, and one around midnight on

12-13 March. Volumes filtered were measured by flowmeter for both drogue and stratified samples.

The transect began at 1930 hours on 13 March and ended at 0530 hours on 15 March, covering 120 km of Bass Strait and 160 km of western shelf waters (Fig. 1). The ship's firemain system, with an intake 2 m below the surface, was used to collect samples. Water from this system was passed through one of a pair of 190 μ m mesh nets and into a bucket. At half-hourly intervals, we switched nets, collected the zooplankton sample and took 1 litre of water from the bucket for chlorophyll, and measured the flow rate by timing the filling of the bucket. Each of the 70 samples represented about 1 m³ of water filtered, and about 4 km traversed.

Chlorophyll samples were collected by filtering 1 litre of water through glass fibre filters, which were frozen and later analysed by fluorometry (Strickland & Parsons 1972).

All zooplankton samples were preserved immediately in buffered 2% formaldehyde. We counted either whole samples or took aliquots to get 300-500 animals. We identified cladocera and copepods to genus or species, and other taxa to a higher taxonomic level; although we counted meroplankton we excluded them from the analysis. We calculated abundances as number per cubic metre; for the stratified series we calculated integrated abundances (number.m⁻²) by dividing the water column into four strata: e.g. the surface sample represented 0-7.5 m, the 15 m sample 7.5-22.5 m, and so on. All parametric tests were based on log (N+1) transformed abundance data. We combined adjacent samples from the transect into nine segments of 8 samples (6 in the last segment) for presentation of data.

RESULTS

Weather conditions were typical of Bass Strait, with sustained wind speeds between 9 and 50 knots. Surface water temperature in Bass Strait was 19-20°C; a thermocline was present at 40-50 m throughout the Bass Strait portion of the cruise.

The drogue meandered within 10 km of the launch position until 10 March, when it abruptly proceeded south westward at 1 km.h⁻¹ (Fig. 1). On 11 March it was retrieved and reset 15 km north east, after which it meandered generally north east.

Zooplankton samples near the drogue (Table 1) con-

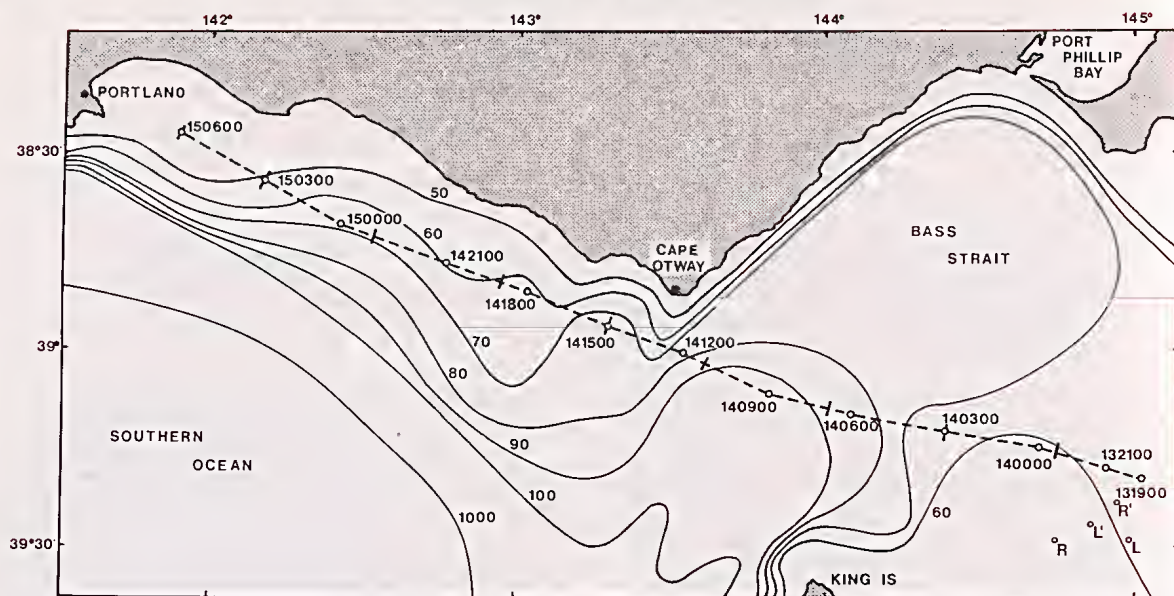


Fig. 1—Location map showing drogue launch and recovery sites and transect. Bars across the transect line delineate segments. Drogue launch 9 March 1983 (L) and recovery 11 March (R); 11 March reset (L) and final recovery 13 March (R).

tained relatively few holoplanktonic species. Although abundances of common taxa were variable, the order of relative abundance was reasonably consistent between samples. There was no trend in abundance with time for any taxon ($p > 0.10$, rank correlation coefficient), nor was the abundance of any taxon significantly different before vs after the drogue was reset ($p > 0.10$, t -test). Euphausiids and *Synopia* (Amphipoda) were absent in samples taken by day; otherwise, day and night abundances were not significantly different.

Abundance patterns that can be seen in the stratified samples (Fig. 2) must be interpreted cautiously since they come from samples taken on one day only. In a few cases, the patterns were clearly the result of vertical migration. For example, *Oithona plumifera*, euphausiids (all that could be identified were *Nyctiphanes australis*), and *Penilia avirostris* were nearly absent and *Calanus australis* and salps (mainly *Thalia democratica*) uncommon, in the surface samples by day.

All of these taxa were common in the surface night samples and in the day samples at greater depths. Limited migration out of the surface layer by day is also suggested for *Paracalanus indicus*. *Synopia* sp. was collected in all night samples and only one 50 m day sample, so these amphipods are probably demersal. None of the other rarer taxa could be identified as vertical migrators. The only clear pattern was that of *Ctenocalanus vanus*, which was collected in low numbers in 3 samples from 30 m and all 4 from 50 m.

Antilogs of standard deviations of the log-transformed abundances for common species in the 30 m samples were at most equal to, and usually less than, the values shown in Table 1 for the 30 m drogue samples.

The temperature profile along the transect (Fig. 3a) shows a thermocline in Bass Strait at about 45 m. A strong surface front southwest of Cape Otway was crossed at 1500 hours on 14 March (sample 40). Shelf waters west of Cape Otway (Fig. 1) were cooler; the dome of $< 14^{\circ}\text{C}$ water below 50 m near the western end of the transect may have resulted from upwelling off the shelf.

Chlorophyll (Fig. 3b) showed no trend except for a sharp peak extending 12 km west from the front. Otherwise values were low, with a mean of 0.24 mg m^{-3} exclusive of the peak.

Geometric mean abundances of taxa in each segment of the transect are presented in Table 2. The most abundant taxa within Bass Strait (i.e. in segments 1-2) were the cladocera *Evadne spinifera* and *Penilia avirostris* and the copepods *Calanus australis* and *Paracalanus indicus*. *Oithona* spp. were abundant throughout the transect, *O. plumifera* over the first 40 km and *O. similis* thereafter. On the western shelf (segments 6-9) the numerically dominant taxa were the copepods *P. indicus*, *Acartia tranteri*, *C. australis* and *Clausocalanus* spp.

Total holoplankton was lower during the day segments (4-6) than during either night because of reduced abundance of many taxa. In particular, the common taxa that showed a clear migratory pattern in the stratified samples were less common or absent by day than at night.

The common taxa can be assigned to groups based on their abundance patterns. The first group consisted of taxa that were abundant only at the beginning of the transect, and absent or rare thereafter. This group included all of the cladocera, chaetognaths, *Pontella* sp.

TABLE 1

ABUNDANCES OF HOLOPLANKTONIC TAXA COLLECTED IN 30 M HORIZONTAL NET SAMPLES AT THE DROGUE.

The asterisk denotes a change in drogue position. Also shown are geometric means and geometric standard deviations (antilogs of standard deviations of log-transformed values), for taxa occurring in at least 10 samples.

Date	8/3	9/3	10/3		11/3		12/3		13/3		Mean	Std. Dev.			
Time	1109	0027	1335	0108	1142	0044	1642	*	2004	1335	0112	1242	1925		
COPEPODA															
<i>Calanus australis</i> (Nauplii)	281	1232	295	2387	2195	1197	2963		728	1025	397	466	401	829	2.3
(C & A)	180	251	83	617	240	248	634		261	293	186	214	171	244	1.7
<i>Paracalanus indicus</i>	367	276	274	741	552	212	350		301	248	330	133	216	303	1.6
<i>Acartia</i> sp.										11					
<i>Clausocalanus</i>	7	8	16	21	12						8				
<i>Ctenocalanus vanus</i>		8													
<i>Corycaeus</i> spp.	7	25	16	103	60	56	241		24	158	93	37	37	47	2.7
<i>Oncaea</i> spp.	22	25	16	21		10			8	23	8	15	7	12	1.8
<i>Oithona plumifera</i>		16	21		36	15	87		55	68	17	22	30	22	2.6
<i>Oithona similis</i>	1288	947	1028	2346	1343	495	1312		1069	2175	1387	613	662	1110	1.6
<i>Sapphirina angusta</i>			5								8				
<i>Clytemnestra rostrata</i>				21	48	35	77		24	56		15	7		
<i>Euterpina acutifrons</i>	7	50	5	41	24	5	44					22	15		
<i>Microsetella rosea</i>		8	5		24		33		8	68	25	7	15		
<i>Copepod nauplii</i>	72	8	36	144	108	10	44		32		42	30	22	31	2.7
CLADOCERA															
<i>Podon intermedius</i>							11					15	7		
<i>Evadne tergestina</i>			5		24	5	55			11	17		7		
<i>Evadne spinifera</i>	7	34	10		24	146	350		158	101	135	111	394	61	4.1
<i>Evadne nordmanni</i>						5	44				8		30		
<i>Penilia avirostris</i>	7	201	72	268	264	96	394		95	90	25	325	387	118	3.4
OTHER TAXA															
Euphausiid calyptopis	7														
furcilia	22	42	5	247		56			111		17		30		
Synopiid amphipod									8		8		15		
Pteropod				21	12										
Siphonophore	14	8	47	103	24	15	11		48	11	17		15	18	2.5
Salp (mainly <i>Thalia</i> <i>democratica</i>)	345	59	367	679	120	116	317		958	158	617	244	141	254	2.3
Larvacean (<i>Oikopleura</i> spp.)	727	461	444	720	972	242	383		721	631	457	244	1189	538	1.6
Chaetognath	50	34	36		168	5	109		32	90	76	74	52	44	2.7
Ctenophore				21											
Total copepod taxa	9	12	12	10	11	10	10		10	10	11	11	11		
Total holoplanktonic taxa	16	19	20	17	19	19	19		17	17	20	17	21		
Total holoplanktonic animals m ⁻³	3410	3693	2786	8501	6250	2969	7459		4633	5217	3870	2587	3835	4285	1.5

and *Corycaeus* spp. The second group comprised the vertical migrators, which were abundant at both ends of the transect but not in the middle during the day. These were *Calanus australis*, *Oithona plumifera*, *Synopia* sp. and euphausiids. The third group consisted of taxa that were abundant only near the end of the transect: *Clausocalanus* spp., *Ctenocalanus vanus*, *Oncaea* spp., *Microsetella rosea* and a group of copepods, rare in

these samples and normally associated with oceanic waters (e.g. *Mesocalanus*, *Calocalanus*, *Eucalanus*, *Pleuromamma* spp., etc.). The remaining taxa showed few similarities in abundance pattern, except that the abundances of *Paracalanus indicus* and *Acartia tranteri* were highly correlated ($r=0.84$, $p<0.01$) in samples taken after the front had been passed.

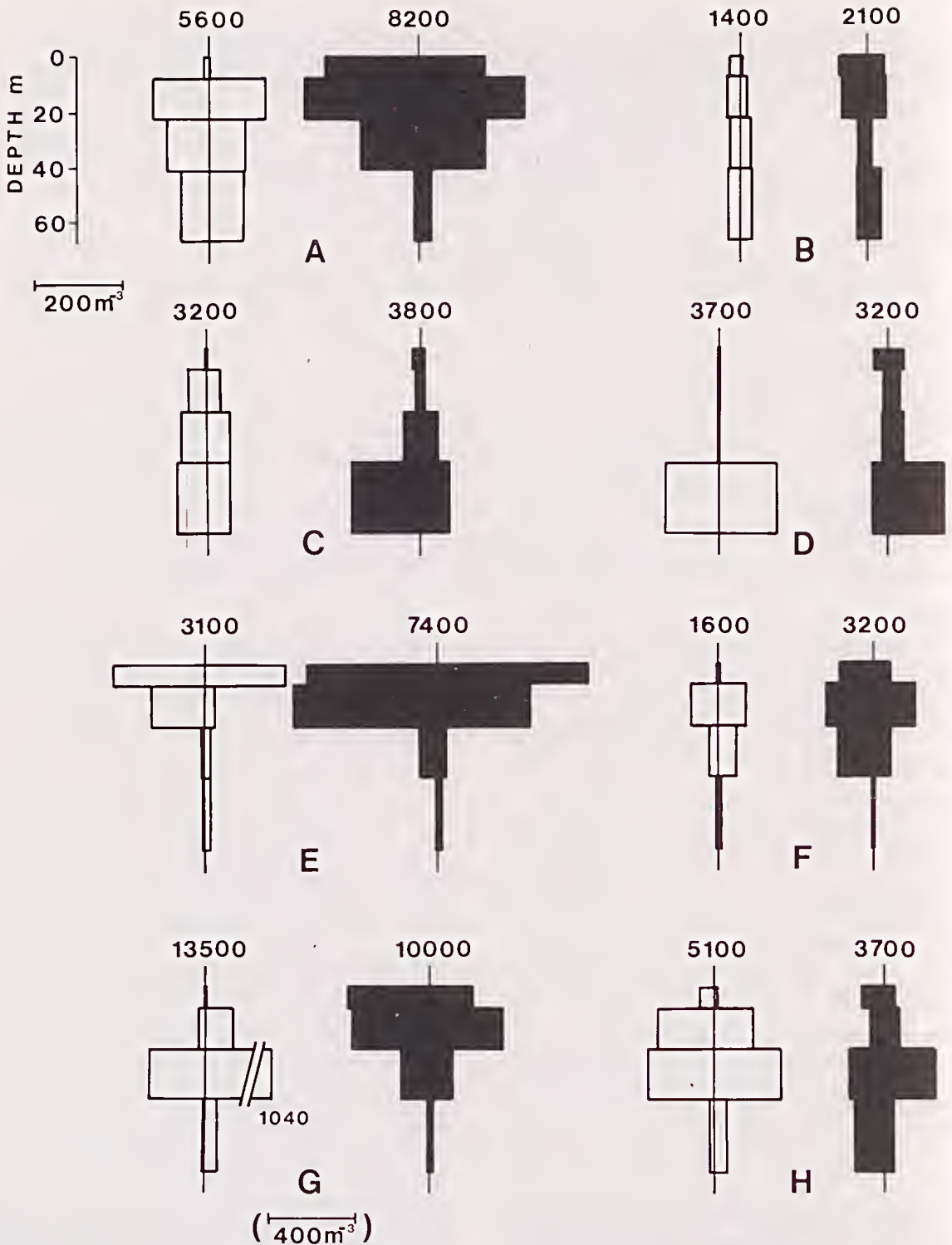


Fig. 2—Vertical distribution of the eight most abundant holoplankton organisms in the stratified samples, 12 March 1983. Each bar represents one of two replicate samples in the depth band indicated; open bars are day samples and filled bars, night. The numbers are mean integrated abundances (number.m²). A, *Calanus australis*; B, *Paracalanus indicus*; C, *Oithona plumifera*; D, Euphausiids; E, *Evadne spinifera*; F, *Penilia avirostris*; G, Thaliacea; H, *Oikopleura* spp.

DISCUSSION

The variability in abundances of common species among the drogue samples was at least as great as, and usually greater than, the variability among the four 30 m stratified samples for the same species. Although we used the drogue to track and, presumably, sample in a single water mass, the water we were actually sampling in, no doubt changed during the drogue series. The presence of a thermocline, strong winds, and the westward displacement of the drogue on 10-11 March all suggest strong current shear and mixing. There was no detectable change in plankton abundances with the change in drogue position, further suggesting that we were in fact sampling in a general region, but not at a point in a water mass.

The differences in species abundances between the three series of samples taken within Bass Strait (Table 3) result largely from differences in mesh size and sample depth. The most abundant species in the 100 μ m drogue samples was *Oithona similis*, which was absent from both the stratified samples and the first group of transect samples. Although it was present in all subsequent transect samples its abundance is probably underestimated because of its small size.

Comparison of abundances on transect segment 1 with surface abundances in the night stratified series reveals few striking differences except that *Oikopleura* and *Thaliacea* are under-represented in the transect samples. This may have resulted from the damage by the pump, since many of the soft bodied animals collected were badly damaged and some may have been destroyed.

Cladocera were very abundant in Bass Strait, and all species had the same abrupt decrease in abundance in segments 2 and 3 of the transect. These decreases cannot be attributed to any observed change in water depth, temperature, stratification or chlorophyll.

Many of the copepod species in Table 2 were oceanic species that occurred only in the last few samples of the transect. These may have been associated with the intrusion of cold water into the shelf; their presence at the surface at night could result from their migrating out of that water mass.

The data listed in Table 3 can be compared with historical data taken with nets of similar mesh size. Noone (1979) found *Paracalanus indicus*, *Oithona* spp., *Calanus australis* and *Acartia tranteri* (as *A. clausi*) the most abundant during summer at the three stations nearest the drogue position. G. F. Watson (pers. comm.) found the most abundant species in the same region in autumn to be *P. indicus*, *O. similis*, *A. tranteri*, *Clausocalanus* spp., and *Ctenocalanus vanus*; *Calanus australis* was rare in those samples. Neritic samples in Bass Strait are dominated by *O. similis*, *Oikopleura* spp., *P. indicus*, *C. australis*, Cladocera and *A. tranteri* (G. F. Watson, pers. comm.), while the zooplankton of nearby Port Phillip Bay is dominated by *P. indicus*, *Oikopleura dioica*, and *A. tranteri* (Arnott 1974, Kimmerer & McKinnon in press). In the earliest record of Bass Strait zooplankton abundances, Dall

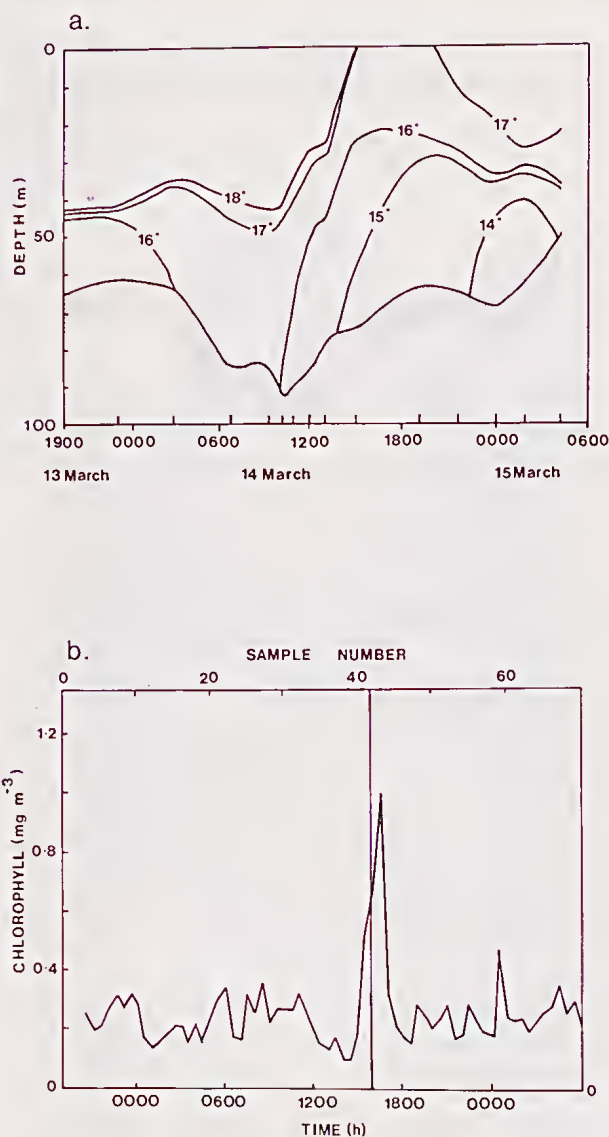


Fig. 3—Data from transect, 12-14 March 1983.

- a: Temperature profiles; tick marks on the ordinate represent points of XBT drops.
- b: Chlorophyll. The vertical line is the position where the front was crossed at the surface.

(1957, 1958) found *C. australis* (as *C. helgolandicus*), *Ctenocalanus vanus*, *Labidocera cervi*, and the amphipod *Parathemisto* sp., to be the most abundant crustacea, but he apparently used nets of larger mesh size.

With the exception of the last two species, which have not been common in any other study, the taxa listed above appear to represent a distinct Bass Strait fauna. *Paracalanus indicus*, *Acartia tranteri* and *Oithona similis* seem to be a neritic element, while *Calanus australis*, *Nyctiphanes australis*, *Oithona plumifera* and *Oikopleura* spp. are more widely

TABLE 2

GEOMETRIC MEAN ABUNDANCES (M^{-3}) OF HOLOPLANKTON TAXA IN NINE SEGMENTS ALONG THE TRANSECT.

Segments 1-8 consist of eight samples, segment 9 of six. Segments 4-6 were day samples, and others night. The front was crossed between segments 5 and 6.

Taxon	Segment								
	1	2	3	4	5	6	7	8	9
COPEPODA									
<i>Calanus australis</i>	213.8	33.4	20.3	3.2	0.6	52.2	96.6	17.1	51.2
<i>Mesocalanus tenuicornis</i>	0	0	0	0	0	0	0	0.1	0
<i>Calocalanus tenuis</i>	0	0	0	0	0	0	0.2	0.9	0.9
<i>Mecynocera clausi</i>	0	0	0	0	0	0	0	0.3	0
<i>Paracalanus indicus</i>	51.9	17.2	72.8	58.5	75.5	444.0	584.5	298.5	248.9
<i>Eucalanus</i> sp.	0	0	0	0	0	0	0	0.2	0
<i>Clausocalanus</i> spp.	1.4	1.3	1.2	1.0	1.3	2.0	16.0	39.7	23.7
<i>Ctenocalanus vanus</i>	0	0.1	0.6	0	0	0.2	1.6	17.5	9.9
<i>Aetidiopsis</i> sp.	0	0	0	0	0	0	0	0.1	0
<i>Chiridius</i> sp.	0	0	0	0	0	0	0.2	0.4	0.2
<i>Centropages australiensis</i>	0.2	0	0	0	0.2	0.7	0.4	0.6	1.9
<i>C. bradyi</i>	0	0	0	0	0	0	0.1	0.5	0.4
<i>Acartia tranteri</i>	1.0	2.1	6.1	15.6	28.9	77.3	78.2	37.6	43.4
<i>Labidocera tasmanica</i>	0	0.2	1.8	0	0.1	1.0	1.3	0.8	0.2
<i>Pontella</i> sp.	1.2	2.0	1.4	0	0.1	0	0	0.1	0.3
<i>Candacia</i> sp.	0.1	0.4	0.1	0	0	0	0	0	0
<i>Pleuromamma gracilis</i>	0	0	0	0	0	0	0.1	0.4	0.1
<i>P. abdominalis</i>	0	0	0	0	0	0	0	0.3	0.3
<i>Corycaeus</i> sp.	18.8	4.3	0.7	0.2	0.1	0	0	0	0
<i>Oncaea</i> sp.	0.8	0.7	0.2	0	0	0	3.0	39.6	26.4
<i>Oithona plumifera</i>	31.3	8.7	1.1	0.3	0	0	1.2	0.5	19.2
<i>O. similis</i>	0	2.4	14.6	16.6	3.0	4.0	4.6	5.1	33.4
<i>O. rigida</i>	0.1	0	0	0	0	0.4	0.2	0.1	0
<i>Sapphirina angusta</i>	0.1	0	0	0	0	0.7	1.3	0.2	0.3
<i>Clytemnestra rostrata</i>	0.5	0.1	0.6	0	0.1	0	0	0	0.4
<i>Microsetella rosea</i>	0	0	0	0	0	0	0	1.8	2.6
<i>Euterpina acutifrons</i>	0	0.1	0	0	0	0	0	0	0
CLADOCERA									
<i>Podon intermedius</i>	2.7	1.2	0	0	0	0	0	0	3.5
<i>Evadne tergestina</i>	1.9	0.7	0	0	0	0	0	0	0
<i>Evadne spinifera</i>	177.7	17.0	0.1	0	0	0	0	0	0
<i>E. nordmanni</i>	2.3	3.2	0.1	0	0	0.4	0	0	0.3
<i>Penilia avirostris</i>	234.2	62.9	0.1	0	0	0	0	0	0
OTHER CRUSTACEA									
<i>Synopia</i> sp.	2.8	1.2	0.5	0	0	0.1	0.2	0.1	0.5
Hyperiid amphipod	0	0	0	0.3	0.1	0	0.1	0.2	0.3
Euphausiid									
<i>Metanauplius</i>	0	0	0.1	0	0	0	1.6	0.4	0
<i>Calypsoptis</i>	0	2.6	15.2	0.2	0.2	0.2	32.4	24.0	17.4
<i>Furcilia</i>	13.9	2.9	2.3	0	0	0.2	4.6	2.4	12.3
OTHER TAXA									
Pteropoda	0	0.2	0	0	0	0	0	0	0
Siphonophora	5.1	2.8	2.0	1.3	1.9	1.9	6.0	5.6	4.0
Thaliacea (mainly									
<i>Thalia democratica</i>)	0.3	1.6	0.2	0	1.4	4.7	3.2	0.5	0
<i>Oikopleura</i> spp.	1.3	6.4	3.4	1.3	1.0	9.5	1.7	2.3	7.5
Chaetognatha	7.8	7.3	1.8	0.4	0	0	0.3	0.3	0.5

TABLE 3
ORDER OF ABUNDANCE OF THE EIGHT MOST ABUNDANT SPECIES IN BASS STRAIT.

For transect samples, only Segment 1 is used. Abundances in stratified samples are based on the entire water column.

Drogue Samples	Stratified Samples	Transect Samples
<i>Oithona similis</i>	Thaliacea	<i>Penilia avirostris</i>
<i>Calanus australis</i>	<i>Calanus australis</i>	<i>Calanus australis</i>
<i>Oikopleura</i> spp.	<i>Evadne spinifera</i>	<i>Evadne spinifera</i>
<i>Paracalanus indicus</i>	<i>Oikopleura</i> spp.	<i>Paracalanus indicus</i>
Thaliacea	<i>Oithona plumifera</i>	<i>Oithona plumifera</i>
<i>Penilia avirostris</i>	Euphausiids	<i>Corycaeus</i> spp.
<i>Evadne spinifera</i>	<i>Penilia avirostris</i>	Euphausiids
<i>Corycaeus</i> spp.	<i>Paracalanus indicus</i>	Chaetognaths

distributed. Bass Strait has complex physical oceanography, and adjoins very different water masses to east and west (Godfrey *et al.* 1980, Jones 1980, Baines 1983, Baines *et al.* 1983). Thus, it should be expected, and it is suggested by the above comparison, that large differences in the order of abundance of the major species should occur between seasons or between cruises.

The front off Cape Otway contained an elevated concentration of chlorophyll, but no species of zooplankton had a peak of abundance at the front. Several species, though, shared a change in abundance pattern after the front was passed. In particular, *Calanus australis*, *Paracalanus indicus*, *Acartia tranteri* and Thaliacea all increased in abundance. In addition, *P. indicus* and *A. tranteri* had closely correlated abundance patterns west of the front, suggesting possible physical control of abundance. The species composition in the samples taken west of the front resembled that of neritic samples from Bass Strait (G. F. Watson pers. comm.), except for the presence of oceanic copepods. Thus, in addition to the fauna typical of open waters in Bass Strait, there is a neritic species group that extends west at least as far as Portland. We expect that this species group will also occur in other southern Australian shelf regions.

The diversity of the Bass Strait zooplankton is low, with 7 species making up 80% of the individuals in the drogue samples. This is typical of continental shelf areas around the world, where relatively few species dominate the numbers (e.g. Deevey 1960, Eriksson 1973, Bainbridge *et al.* 1978, Peterson *et al.* 1979, Stepien *et al.* 1981).

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DESCRIPTION OF THE MALE OF *LABIDOCERA CAUDATA* NICHOLLS (COPEPODA: PONTELLIDAE) WITH REMARKS ON THE FEMALE

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ABSTRACT: We describe the male of *Labidocera caudata* Nicholls (Copepoda: Pontellidae), known previously from only two female specimens, and expand the description of the female. *L. caudata* appears to be a late summer inshore species.

Labidocera caudata is known from only two female specimens, taken by Nicholls (1944) in Spencer Gulf, South Australia. We have found *L. caudata* in Western Port, Victoria, and here complete the description of both sexes.

All material was collected in horizontal surface plankton tows with 50 cm nets of either 150, 200 or 333 μ m mesh. We measured and dissected specimens in glycerol, and mounted them on microslides in polyvinyl lactophenol. Drawings were prepared using a Wild M20 phase contrast microscope and camera lucida. Further examination was made with an Olympus Nomarski microscope. Material has been deposited in the Museum of Victoria (male J3137, female J3138 dissected on slides, bodies separate in vials J3139, J3140 3 females, 3 males in vials) and South Australian Museum (6 females, 2 males Reg. No. C3988).

SYSTEMATICS

Labidocera caudata Nicholls 1944 Figs 1, 2

MATERIAL EXAMINED: Sixty-one females and 12 males Freeman Point (38°22.8'S, 145°27'E) 22 Dec. 82; 3 females Warnet (38°13.7'S, 145°18.3'E) 29 Mar. 84; 7 females, 5 males Rhyll (38°27.8'S, 145°19.2'E) 16 April 84; 2 females, 3 males Rhyll 17 April 84; 4 females 1 male Rhyll 18 April 84; 2 females Rhyll 9.5.84.

DESCRIPTION OF MALE: Mean body length to end of furcal rami 2.29 mm \pm 0.1 S.D. (range 2.15-2.44) based on 9 specimens. Head rounded in dorsal view (Fig. 1a), with a slight prominence posterior to the origin of the antennules. In lateral view (Fig. 1b) there is an indentation at about the mid-length of the cephalosome. The dorsal eye lenses are large and close together. Underlying the lenses is a large densely pigmented block of tissue; a second, similar but smaller block is located in the protuberant medioventral eye. The rostrum (Fig. 1c) is large and postero-ventrally directed, the bifid rami separated at their base by about their own length. There are two lateral setules on the fourth thoracic segment, and four on the fifth thoracic segment. The posterior corners of the fifth thoracic segment are almost symmetrical, the right being very slightly longer. An additional, much smaller setule is borne near the apex of the thoracic corners (Fig. 1d).

The urosome (Fig. 1d) is 5 segmented, with the genital segment slightly asymmetrical, the left side slightly expanded.

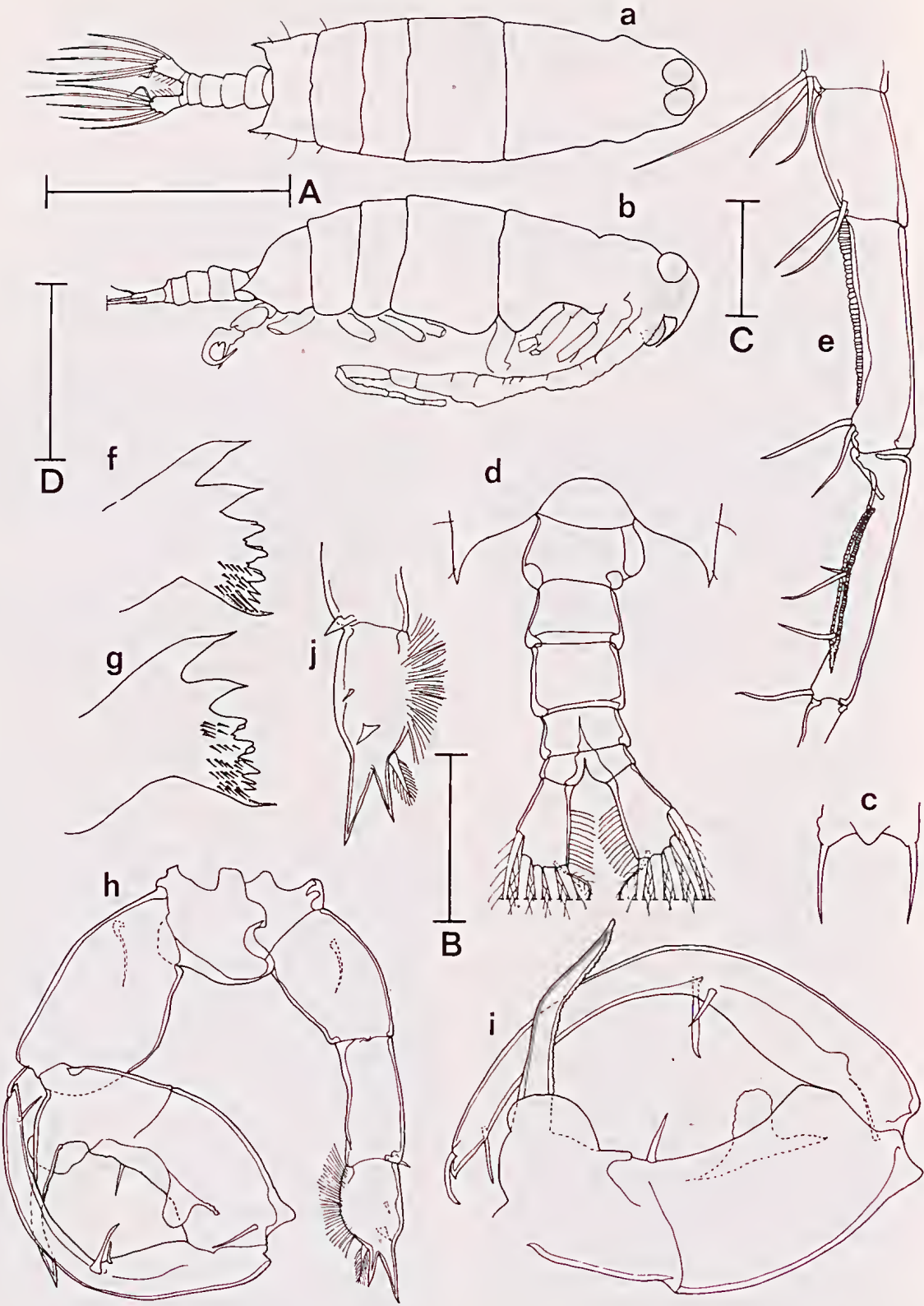
Segment 17 of the right antennule (Fig. 1e) is 1.64 times as long as wide, and bears two setae distally, and no denticles. Segment 18 is 3.67 times as long as wide, and has along the anterior margin a plate bearing about 27 denticles and two setae distally. Fused segments 19-21 are about 6 times as long as wide, and bear a double row of about 60 denticles along the anterior margin. Two setae are borne at about mid-length, one at about 75% length, and one distally.

The mandibles (Fig. 1f, g) have two well developed and broadly spaced single teeth, three median bicuspid teeth, and a pair of sharply pointed single teeth adjacent to the basal seta. Both surfaces of the mandible blade have swathes of small spinules, those in the region of the basal seta more strongly developed.

The coxa of right leg 5 (Fig. 1h) has a plumose seta on the posterior face. Chela of right leg 5 (Fig. 1h, i) with the 'thumb' about mid-length of the segment and arising near the base of exopodite 1. It is surrounded basally by a lamellate collar and the concave face has a rough surface. Exopodite 1 has a fold at a little over 30% of its length, giving the impression of a segment. A small seta arises on the inner border at about this point. At about 70% the length of the segment there is a rough blunt lamellate process on the anterior face. At the distal end of the segment there is inwardly directed seta.

The second exopod segment forms the 'finger' of the chela. The proximal 40% of the segment is lamellate on the inner side, at the distal extremity of which are two small thick setae, the distal 60% of the segment is evenly curved. On the distal end of the segment there is a seta on the inner margin, and on the outer margin a sub-terminal seta.

Left leg 5 basipod (Fig. 1h) has a plumose seta on the posterior face. The first exopod segment is unornamented except for a small triangular spine on the outer distal corner. The second exopod segment (Fig. 1h, j) is hirsute on the inner margin. A small triangular spine is borne at about mid-length of the segment on the posterior face; there is a second similar but stronger spine at about 75% the length of the segment on the same face. Terminally the segment is produced into two large triangular processes, adjacent to which there is a single plumose seta on the inner margin.



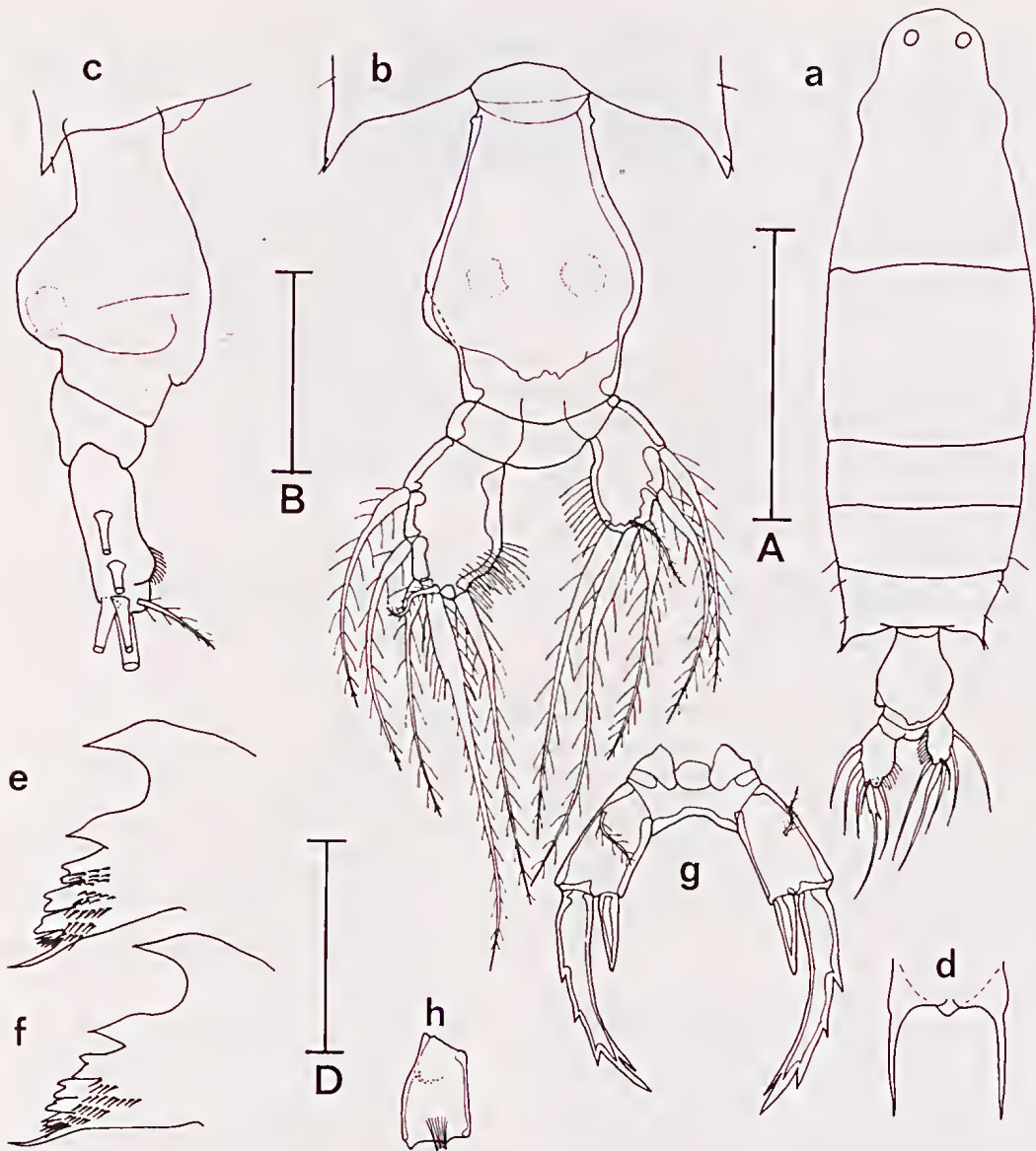


Fig. 2—*Labidocera caudata* Nicholls 1944 female: a, dorsal (scale A); b, urosome, dorsal (B); c, urosome, lateral (B); d, rostrum (B); e, right mandible blade, inner surface (D); f, left mandible blade, outer surface (D); g, leg 5, posterior (B); h, basis of left leg 5, anterior (B).

Scale bars as for Fig. 1.

DESCRIPTION OF FEMALE: Mean body length to end of furcal rami $2.65 \text{ mm} \pm 0.09 \text{ S.D.}$ (range 2.48-2.81) based on 19 specimens. Form of the body (Fig. 2a) similar to that of the male, but the dorsal eye lenses are smaller and separated by more than two times their diameter. In life, the first thoracic segment of most females was

densely coloured red brown. Rostrum similar to that of the male but more attenuated, the rami separated by slightly more than their own length. The fifth thoracic segments are almost symmetrical, the left being very slightly longer. The mandible blades (Fig. 2e, f) are similar in form to the male.

Fig. 1—*Labidocera caudata* Nicholls 1944 male: a, dorsal (scale A); b, lateral (A); c, rostrum (B); d, urosome, ventral (B); e, segments 17 to 21 of right antennule (C); f, right mandible blade, inner surface (D); g, left mandible blade, outer surface (D); h, leg 5, anterior (C); i, right leg 5 chela, posterior (D); j, terminal segment of left leg 5, posterior (D).

Scale bars: A 1.0 mm; B 0.25 mm; C 0.10 mm; D 0.10 mm.

The urosome (Fig. 2b, c) is two segmented. The genital segment has a large lobe produced posterior-dorsally, the margin of which is irregular. The anal segment is small and asymmetrical, the left hand side being longer than the right. The left caudal ramus is 1.37 times longer than the right. The setae on this ramus all have a bulbous basal portion and a longer attenuated distal portion. The longest apical seta is produced into two spiniform processes at the distal extreme of the bulbous basal portion. The ramus is hirsute on the dorsal and medial faces. The right ramus is similar in form but smaller, the hairs are limited to the medial face of the ramus.

The fifth legs (Fig. 2g) are slightly asymmetrical, the right exopod slightly longer than the left. There is a seta on the posterior face of each basipod. The anterior face of each basipod (Fig. 2h) has a distal patch of long setules. The endopods are simple triangular segments. The exopods have three sharp lateral prominences, a sharp terminal point, and a single weak subterminal point on the medial face.

All females had spermatophores, the form of which was illustrated by Nicholls (1944).

COMPARISON WITH HOLOTYPE: The holotype (South Australian Museum, Reg. No. C3983) is a female specimen 2.24 mm in length, mounted on a single microslide, the body and urosome intact under one coverslip, and the complete set of appendages under another. The endopod of the fifth leg of the holotype has a distal portion which is more strongly tapered than in our material, at the base of which is a very small spinule. The basipod seta and patch of setules are present on the holotype, though not figured in Nicholls' (1944) description. In other respects the holotype is similar to the Western Port material, though at 2.24 mm in length it is smaller.

REMARKS: In a one-year (1982-83) study of the distribution of zooplankton in Port Phillip Bay and Western Port (Kimmerer & McKinnon in prep.) *Labidocera caudata* was abundant in Western Port from October to January 1983. In 1982-83 it was the only species of *Labidocera* in Western Port. In late March to May 1984 we found *L. caudata* to be quite common in Western Port, at Warneet and Rhyll. It co-occurred in 1984 with two other species of *Labidocera*, *L. cervi* Kramer 1895 and *L. tasmanica* Taw 1974. *L. cervi* is widely distributed in southeastern Australia and New

Zealand (Greenwood 1979) and is a resident in Port Phillip Bay. *L. tasmanica* is a Bass Strait resident that occasionally penetrates into the bays. *L. caudata* did not occur in Port Phillip Bay at these times. Nicholls' type material was collected in March 1938. *L. caudata* therefore seems to be a late summer species, which is limited in Western Port to the inner bay.

L. caudata, *L. cervi* and *L. tasmanica* all belong to the super species *detruncata*, reviewed by Greenwood and Othman (1979). Males of *L. caudata* are characterised by the structure of the fifth leg: the lamellate collar surrounding the base of the 'thumb', and the rough lamellate process at about 70 per cent of the length of the first exopodite segment, are both distinctive.

L. caudata appears to be most closely related to *L. madurae* A. Scott 1909, based on the structure of both male and female fifth legs.

ACKNOWLEDGEMENTS

We thank the South Australian Museum for the loan of the type material. This work was supported by M. S. T. Grant #83/1325.

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PROCEEDINGS
OF THE
ROYAL SOCIETY OF VICTORIA

Volume 96

NUMBER 4

ROYAL SOCIETY'S HALL
9 VICTORIA STREET, MELBOURNE 3000

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NEW PLACODERM FISHES FROM THE EARLY DEVONIAN BUCHAN GROUP, EASTERN VICTORIA

By JOHN A. LONG

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ABSTRACT: Three new placoderms are described from the McLarty Member of the Murrindal Limestone (Early Devonian, Buchan Group). *Murrindalaspis wallacei* gen. et sp. nov. is a palaeacanthaspidoid characterized by having a high median dorsal crest and lacking a median ventral keel. *M. buirdi* sp. nov. differs from the type species in having a low median dorsal crest and a median ventral groove. *Taeniasosteus maclartiensis* sp. nov. differs from the type species *T. novaustrocambricus* White in the shape of the posterior region of the nuchal plate, the presence of canals between the infranuchal pits and the posterior face of the nuchal plate, the shape of the paranuchal plate, and the development of the apronic lamina of the anterior lateral plate.

The placoderms, *Arenipiscis westolli* Young, *Errolosteus* cf. *E. goodradigbeensis* Young, *Wijdeaspis warrooensis* Young, are recorded from the Buchan Group indicating close similarity to the ichthyofauna of the contemporaneous Murrumbidgee Group, New South Wales.

Few fossil fishes have been studied from the Early Devonian Buchan Group. McCoy (1876) described some placoderm plates from this region as *Asterolepis ornata* var. *australis*, which Chapman (1916) queried when presenting a description of a placoderm skull from Buchan. Chapman identified this specimen as a phlyctacnioid, *Phlyctacnaspis confertituberculatus*, but Hills (1936b) assigned the skull to *Coccosteus*. Stensiö (1945) recognized differences between the parasphenoid of *Coccosteus* and the Buchan specimen and erected *Buchanosteus* for the latter. Additional material of *Buchanosteus* has since been found from the Murrumbidgee Group, New South Wales, making this genus one of the best known Early Devonian euarthrodires (White 1952, White & Toombs 1972, Young 1979). The only other fish described from Buchan is a mandible of the dipnoan *Dipnorhynchus sussmilchi* (Hills 1936a, Thomson & Campbell 1971). This paper describes placoderm fish material recovered from the Buchan Group during Monash University third year geology field mapping trips as well as some found by geology honours students from both Melbourne and Monash Universities (Long 1983b).

The material was prepared using acetic acid with dilute polyvinylbuterol to strengthen the exposed bone. All specimens were found in the uppermost McLarty Member or the lowermost Rocky Camp Member of the Murrindal Limestone, with the richest concentration of vertebrates occurring near the contact of the McLarty and Rocky Camp Members on the eastern face of Rocky Camp Hill (Fig. 1). In addition to the macrovertebrate remains rich concentrations of microvertebrate fossils were recovered from the residues during preparation, and these have been forwarded to Dr. S. Turner (Queensland Museum) for detailed study. Amongst these are several types of acanthodian and elasmobranch scales similar to forms described from the Murrumbidgee Group by Giffin (1980). Recently a jaw of a new ischnacanthid acanthodian was found in residues from the Rocky Camp Member (under current study by the author). Lower Devonian macrovertebrates have also

been described from the Murrumbidgee and Mulga Downs Groups in New South Wales and the Cravens Peak Beds in Queensland, with numerous sites yielding microvertebrate assemblages (Long 1982, 1983b, Turner *et al.* 1981, Long & Turner 1984).

Specimens are housed in the following institutions: CPC, Commonwealth Palaeontological Collections, Bureau of Mineral Resources, Canberra; MUGD, Geology Department, Melbourne University; and NMV, Museum of Victoria, Melbourne.

SYSTEMATIC PALAEONTOLOGY

Subclass PLACODERMI McCoy 1848

Superorder PETALICHTHYOMORPHA Miles & Young 1977

Order PETALICHTHYIDA Jaekel 1911

Wijdeaspis warrooensis Young 1978

Fig. 4C

MATERIAL: A piece of trunk shield comprising the right spinal plate and a small sliver of the anterior lateral plate. NMVP159825, collected Dr. R. E. Fordyce, February, 1981.

OCCURRENCE: The uppermost division of the McLarty Member of the Murrindal Limestone, immediately northeast of Rocky Camp Quarry, north of Buchan.

REMARKS: The specimen is identified as belonging to *Wijdeaspis* because the spinal shows a relatively high number of ornamental ridges (9-10) which are formed of closely packed tubercles arranged in rows. On this basis Young (1978, p. 112) distinguished *Wijdeaspis* spinal plates from those of *Lunaspis* species. The Buchan specimen is almost identical with that of *Wijdeaspis warrooensis* figured by Young (1978, figs 2E, 8B).

Order RHENANIDA Broili 1930

Suborder PALAEACANTHASPIDOIDEI Miles & Young 1977

Family WEEJASPERASPIDAE White 1978

DIAGNOSIS: Palaeacanthaspidoids having a well developed median dorsal crest on the median dorsal plate, which has a posterior face with a smooth medial

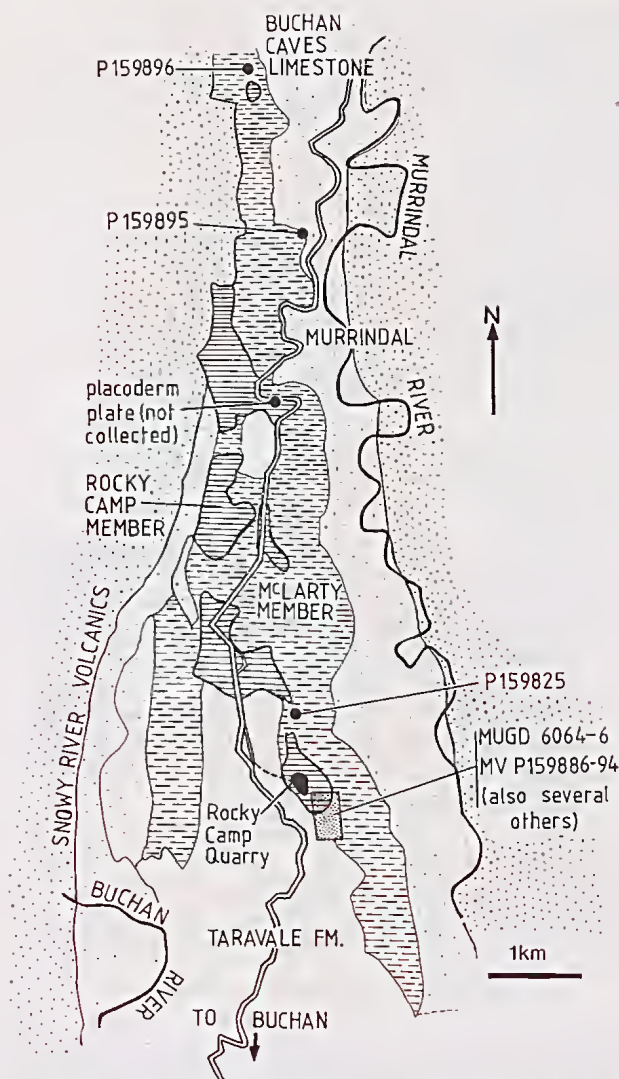


Fig. 1—Locality map of placoderm fossils collected in the Buchan region. Geology from Teichert & Talent (1958).

prominence. Median dorsal plate with a B/L index approximately 80. Coarse ornamentation consisting of short ridges and pointed tubercles each with well defined grooves.

REMARKS: White's diagnosis (1978) has been modified to incorporate features of the new genus from Buchan. *Weejasperaspis* White 1978 and *Murrindalaspis* gen. nov. are similar in the proportions of the median dorsal plate, in their median dorsal crests and in the morphology of the dermal ornamentation; they differ chiefly in the well-developed median ventral ridge on *Weejasperaspis* only, and in the size of tubercles of the external ornament.

Murrindalaspis gen. nov.

ETYMOLOGY: After the settlement of Murrindal, north of Buchan.

DIAGNOSIS: A weejasperaspid of moderate size having a median dorsal plate with a smooth ventral surface which may have a median ventral groove developed; dermal ornamentation of short ridges, approximately one-third as long as broad, on the dorsal surfaces with pointed stellate tubercles densely concentrated near the anterior and posterior margins; median dorsal crest developed; a short dorsal transverse sensory line canal situated at the anterior base of the median dorsal crest; the posterior face of the median dorsal crest with a smooth median prominence throughout.

TYPE SPECIES: *Murrindalaspis wallacei* sp. nov.

REMARKS: This palaeacanthaspid is similar to *Weejasperaspis gavini* White (1978) but differs in the absence of the median ventral keel on the median dorsal plate. *Palaeacanthaspis* Stensiö 1944 also possesses a median dorsal crest but differs from both *Murrindalaspis* and *Weejasperaspis* in possessing a large nutritive foramen for the crest on the ventral surface of the median dorsal plate, and by its simple tubercular ornamentation. Of the remaining described palaeacanthaspids none has a well developed median crest; where the median dorsal plate is unknown (*Brindabellaspis* Young 1980, *Romundina* Ørvig 1975, *Kimaspis* Mark-Kurik 1973a, *Kolymaspis* in Denison 1978) *Murrindalaspis* is distinguished by the characteristic dermal ornamentation.

Murrindalaspis wallacei sp. nov.

Figs 2A, D, E, G, 3, 8C, D

ETYMOLOGY: After Mr. M. Wallace, Dept. Geology, University of Tasmania, who discovered several fishes from the Buchan area in 1982, including the type specimen of *Murrindalaspis* gen. nov., and kindly allowed me to study the material.

DIAGNOSIS: A member of *Murrindalaspis* with a median dorsal plate having a high median dorsal crest which is strongly curved posteriorly and tapers narrowly at its apex. Ventral surface of median dorsal plate smooth, and there are paired prominences developed at the posterior end of the ventral surface near the base of the crest. Ratio of median dorsal crest height/plate length approximately 64.

HOLOTYPE: MUGD6066 (Figs 2A, D, E, G, 3), an almost complete median dorsal plate from the top of the McLarty Member of the Murrindal Limestone from the vicinity of Rocky Camp Quarry, north of Buchan (Fig. 1).

DESCRIPTION: The holotype is almost complete, missing only the top of the crest and a small part of the left anterolateral corner. It bears a high, slender median dorsal crest (cr.d) which starts approximately 28% of the plate length from the anterior margin, and extends backwards beyond the level of the posterior margin (Fig. 3). In profile the crest is strongly curved, being proportionately much narrower than the broad crest of *Weejasperaspis* (Fig. 8). The anterior margin of the plate has a short median convexity and lateral to this region the anterior margin extends forward at an angle of about

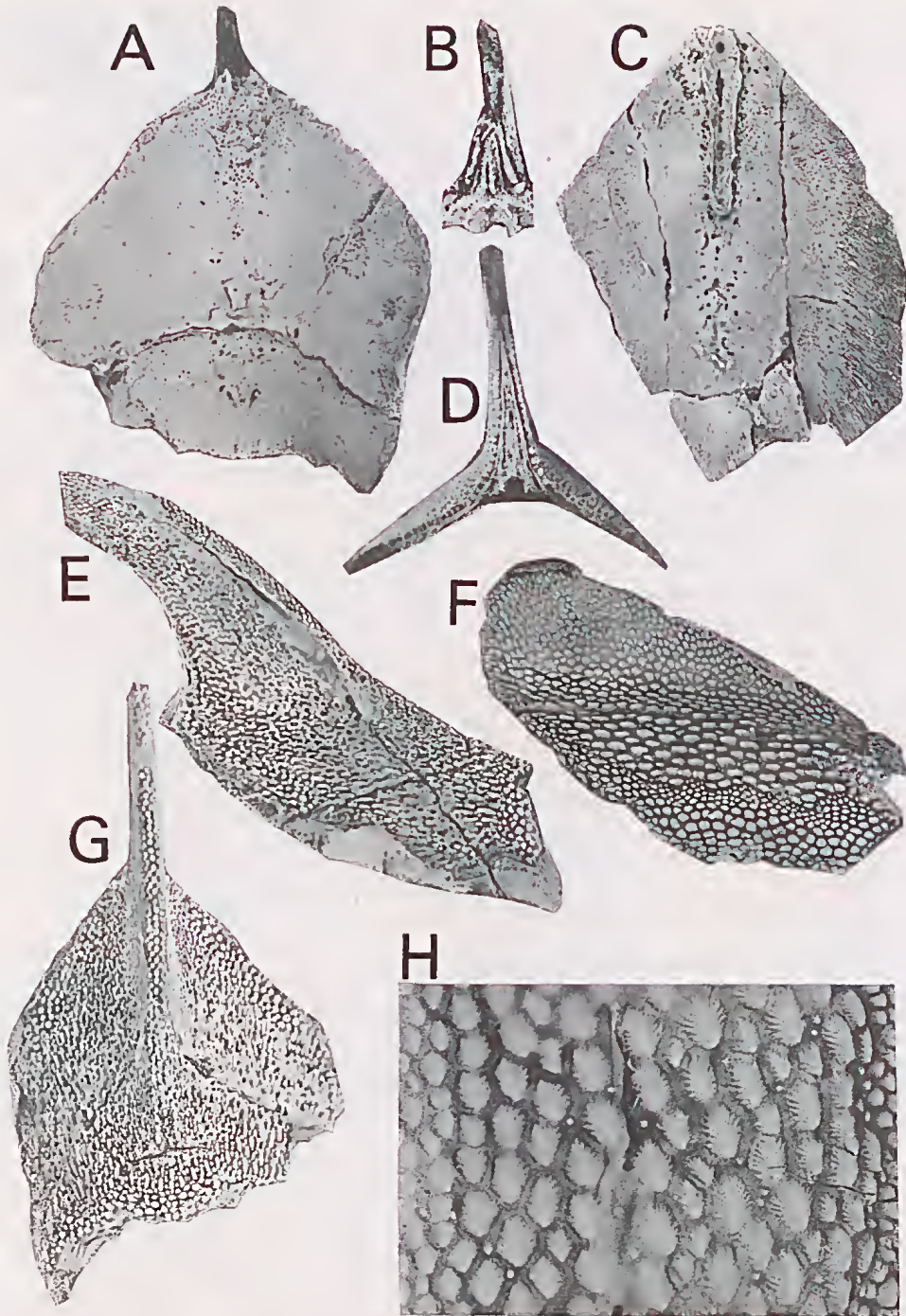


Fig. 2—*Murrindalaspis* gen. nov., Emsian, Buchan. A, D, E, G, *M. wallacei* sp. nov., MUGD6066. Holotype median dorsal plate in A, ventral, D, posterior, E, right lateral and G, dorsal views, $\times 1$. B, C, F, H. *M. bairdi* sp. nov., NMVP59892. Holotype median dorsal plate in B, posterior, C, ventral, and F, right lateral views. H, detail of dermal ornamentation. B, $\times 2$; C, F, $\times 1$; H, $\times 4$. All specimens whitened with ammonium chloride.

40° to the lateral margin of the plate. There is a narrow overlap platform (ant.oa) along the extent of the anterior margin. In dorsal view the plate has constant breadth in its anterior half and tapers posteriorly towards the posterior processes (ppr). The posterolateral margin is straight, without the irregular notches seen on *Weejasperaspis*. There is a short transverse sensory line canal (dg) situated just anterior to the base of the crest and extending for a short distance laterally (Fig. 3D). The ventral surface of the plate is smooth with slightly striated lateral margins where there is overlap with the anterior and presumably posterior dorsolateral plates (oa.ADL). In the midline of the ventral surface there is a concentration of small vascular pores (vas). Two larger foramina occur at the anterior end, below the position of the transverse dorsal sensory canal, probably for innervation of this sensory line. Posteriorly a median process (mpr) is developed, behind which are paired protuberances (ppr) marking the base of the crest. In lateral view, these paired processes extend behind the ornamented external surface. White (1978, p. 159) noted the presence of a process on the posterior face of the median dorsal of *Weejasperaspis* suggesting an articulation for either a posterior median dorsal plate or body scute. As posterior median dorsal plates are only known in antiarchs, and body scutes tend to lie flat on the dorsal ridge of the trunk it is more probable that this region was an attachment area for a dorsal fin support. The posterior margin of the median dorsal spines of some pycnodontids are grooved for attachment of the dorsal fin support in a similar fashion (e.g. *Rhamphodopsis* Miles 1967). In posterior view (Fig. 3B) the base of the median dorsal crest of *M. wallacei* shows a smooth median vertical thickening (mth) flanked on each side by well defined grooves, which deepen towards the base of the crest. A short distance above the paired processes there is a central foramen (for). As the plate was broken in two halves when collected it can be noted that there is a large canal inside the plate running along the base of the crest.

The ornamentation of *Murrindalaspis* (Fig. 2H), is quite distinctive as is this feature on many palaeacanthaspid. In the development of small ridges and tubercles with distinctive ridges it is superficially similar to *Weejasperaspis*. It differs from this genus in that the ridges are shorter (average approximately one-third as long as broad) and predominate on the dorsal surface of the plate with high, pointed stellate tubercles in dense concentrations at the anterior and posterior margins. The crest has closely packed tubercles which grade into short, small ridges on its flanks. All ridges of ornament on the plate have a rostrocaudal alignment, although on the lower part of the crest these form an angled pattern pointed towards the anterior end of the base of the crest.

Murrindalaspis bairdi sp. nov.

Fig. 2B, C, F, H

ETYMOLOGY: After Mr. Robert Baird, Earth Sciences Dept., Monash University, who found the holotype specimen in July, 1983.

DIAGNOSIS: A *Murrindalaspis* having a median dorsal plate which bears a low median dorsal crest. The ventral surface of the median dorsal plate has a well defined median ventral groove in the posterior half of the plate.

HOLOTYPE: An almost complete median dorsal plate, NMVP159893 from the base of the Rocky Camp Member of the Murrindal Limestone, on the southeastern face of Rocky Camp quarry hill, north of Buchan (Fig. 1).

REMARKS: The two species of *Murrindalaspis* are known only from median dorsal plates, yet as they both bear the same distinctive type of dermal ornamentation it is assumed that they are congeneric. The differences seen in the two species are not intraspecifically variable characters. In the antiarch *Bothriolepis* there are interspecific variations in the heights of median dorsal crests and in the presence or absence of median ventral grooves (Miles 1968, Long 1983a). It is unfortunate that palaeacanthaspidoids are too rare as fossils to test the variability of the median dorsal plate morphology within and between species. The two median dorsal plates of *Murrindalaspis* are of about the same size which indicates that the differences seen between the two forms are not attributable to growth changes. As the two species occur in different lithofacies, *M. bairdi* in clean biosparite and *M. wallacei* in interlayered micritic packstones and mudstones, it is possible that the differences in crest height could relate to the degree of turbulence or current activity which predominated in the differing palaeoenvironments.

DESCRIPTION: The holotype median dorsal plate is missing the anterior margin and left anterolateral corner. Although the left side of the crest is slightly damaged the full extent of the crest is shown on the right side of its dorsal margin.

The plate (Fig. 2F) has a slender, broad median dorsal crest which runs along the entire preserved length of the plate. The dorsal margin is gently curved with the crest height being approximately 51% of the overall height of the plate. The ratio of crest height to plate length (as preserved) is 31. The form of the plate in dorsal view is the same as for *M. wallacei* (compare Fig. 2A, C). The posterior face of the plate has a short median thickening which is bordered by a narrow ridge (Fig. 2B). The median thickening extends ventrally to meet the lateral sides of the ventral median groove. The ventral aspect (Fig. 2C) shows this groove extending for 40% of the plate length from its posterior extent. Anterior to the median ventral groove are numerous vascular foramina, as on the ventral surface of *M. wallacei* (Fig. 2A). The dermal ornamentation of *M. bairdi* is slightly coarser than that of *M. wallacei* just lateral to the base of the crest, and on the lateral sides of the crest (Fig. 2E, F) but is otherwise virtually indistinguishable on the two species.

Order EUARTHRODIRA Gross 1932

Suborder PHLYCTAENIOIDEI Miles 1973

Infraorder BRACHYTHORACI Gross 1932

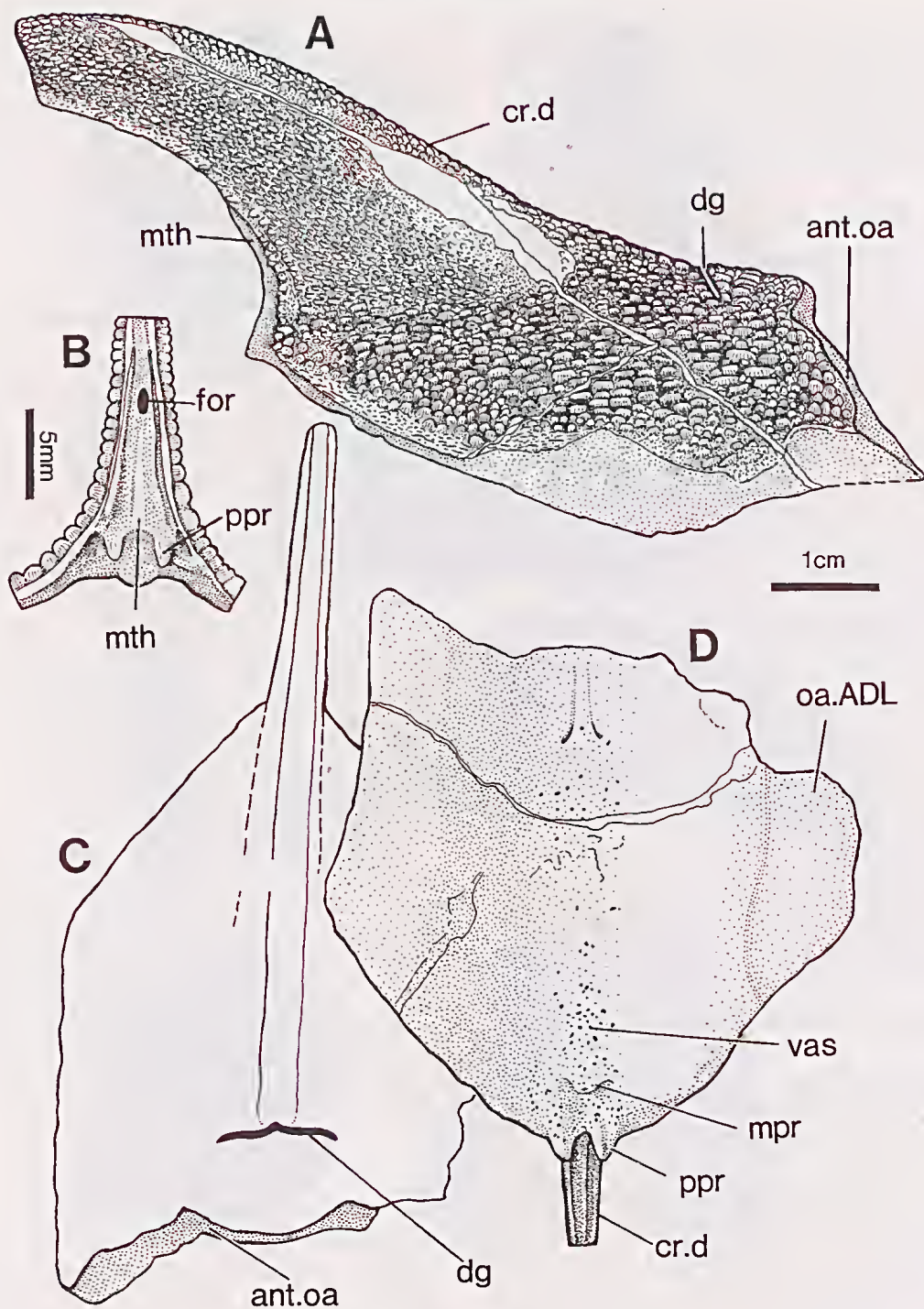


Fig. 3—*Murrindalaspis wallacei* gen. et sp. nov., Emsian, Buchan. Holotype median dorsal plate in A, right lateral, C, dorsal, and D, ventral views. B, detail of posterior face of median dorsal crest. MUGD 6066. ant.oa, anterior overlap surface; oa.ADL, overlap area for anterior and possibly posterior dorsolateral plates; cr.d, median dorsal crest; dg, dorsal transverse sensory-line groove; for, posterior foramen of crest; mpr, median ventral process; mth, median thickening; ppr, paired posterior processes at base of crest; vas, vascular foramina.

REMARKS: These taxa were defined by Young (1979, p. 344, 345) and Long (in press) has amended this definition of the Euarthrodira to include phyllolepid. The following section records taxa from the Buchan Group not previously reported, except for *Buchanosteus confertituberculatus* (Hills 1936b, White 1952, Young 1979).

Arenipiscis westolli Young 1981b

Fig. 4F

MATERIAL: An almost complete nuchal plate, NMVP159885, collected by Mr. Ken Simpson, 1975 from a road cutting near Murrindal, north of Buchan. Although the stratigraphic horizon was not indicated on the label, the lithology suggests that the specimen came from the thinly bedded, fossiliferous McLarty Member of the Murrindal Limestone. Other fish fragments have been found in this region on the road outcrop immediately north of Henham Homestead.

REMARKS: The nuchal plate is referred to *Arenipiscis westolli* on the basis of relative proportions, the presence of a conspicuous median ventral depression and by the fine grained tubercular ornamentation.

DESCRIPTION: The posterior median region of the plate is not preserved, although the shape of the lateral posterior margins is apparent. Other features characteristic of *Arenipiscis* seen on the Buchan specimen are the narrow anterior region of the plate, numerous nutritive foramina along the median ventral depression, well defined infranuchal pits (only partly preserved) and the broad overlap areas for the paranuchal plates. The Buchan specimen has an estimated B/L index of 88 (the anterior margin and broadest lateral extremities are not complete). As the New South Wales type material does not include a complete nuchal plate, proportions can only be estimated from Young's restoration (1981b, figs 5, 6), where the nuchal is slightly broader than long.

Errolosteus cf. *E. goodradigbeensis* Young 1981b

Fig. 4A

MATERIAL: Almost complete anterior dorsolateral plate, NMVP159894 from the upper part of the McLarty Member of the Murrindal Limestone in the vicinity of Rocky Camp Quarry, north of Buchan.

REMARKS: This genus is easily recognized by the characteristic dermal ornamentation of concentric ridges bearing small tubercles. Young (1981b) described the type species from an imperfect headshield, an anterior lateral plate and a posterior ventrolateral plate. The anterior dorsolateral plate from Buchan has a shape compatible with that of the dorsal margin of the anterior lateral of *E. goodradigbeensis*, and for this reason it is provisionally referred to this species until more material is recovered.

DESCRIPTION: The anterior dorsolateral plate is higher than long, as in *Buchanosteus* and most phlyctaenoids (Denison 1978). The plate has an overall H/L index of 153. The anterior margin of the plate is longer than the

rounded posterior margin. The overlap area for the median dorsal plate extends for just under half of the plate length with the ventral overlap area for the anterior lateral plate extending for 80% of plate length. The external ornamented area of the plate is broadest anteriorly, then narrows before becoming broader at the posterior margin. The articular condyle is a short, rounded process as in other primitive brachythoracids.

Taemasosteus White 1952

DIAGNOSIS: As in White, 1978, p. 184.

TYPE SPECIES: *Taemasosteus novaustrocambricus* White 1952.

REMARKS: White (1952) established this genus upon a single left paranuchal plate and recently redescribed the taxon from over eighty plates (White 1978). *Taemasosteus novaustrocambricus* is a common element in the Taemas-Wee Jasper fauna, and has been reported at Buchan (Young 1979, p. 311) although details were not given. This report was based on NMVP41829, a left paranuchal attached to part of the nuchal (Fig. 6A), collected by a Mr. Goodwin from the Rocky Camp member in the early 1970s and prepared by Dr. G. C. Young. In the recently collected material from Buchan *Taemasosteus* is common, although differences in proportion and morphology indicate that some of the material constitutes a new species, whereas other plates are indistinguishable from the type species. All the Buchan specimens resemble *Taemasosteus novaustrocambricus* in their large size, thickness, dermal ornamentation and approximate shape, and are referred to the genus on these characters.

The following plates of *Taemasosteus*, collected near Buchan, are indistinguishable from the type species, *T. novaustrocambricus*: NMVP159889, an imperfect left central plate (Fig. 4E); NMVP159886, imperfect left paranuchal plate (Fig. 6B); NMVP161865, an imperfect right interolateral plate (Fig. 7d); and NMVP159888, a posterior region of the median dorsal plate (Fig. 7B, C). These may turn out to belong to the new species described below but this cannot be shown unless articulated material is found. For the present these specimens are referred to *T. novaustrocambricus*.

Taemasosteus maclartiensis sp. nov.

Figs 4B, D, 5, 6A, 7A, E, 8A

ETYMOLOGY: After the McLarty Member of the Rocky Camp quarry where most of the specimens were found.

DIAGNOSIS: A member of *Taemasosteus* having a nuchal plate which is not strongly raised at the occipital end, and with short, deep grooves connecting the posterior face of the nuchal plate to the large infranuchal pits. Posterior margin of the nuchal plate slightly concave, much straighter than for *T. novaustrocambricus*. Paranuchal plate with straight posterior margin forming an angle of 50° with the suture to the nuchal plate. Anterior lateral plate with 4 toothed ridges on the apronic lamina which is inturned at an angle of 65° to the lateral lamina of the trunkshield.

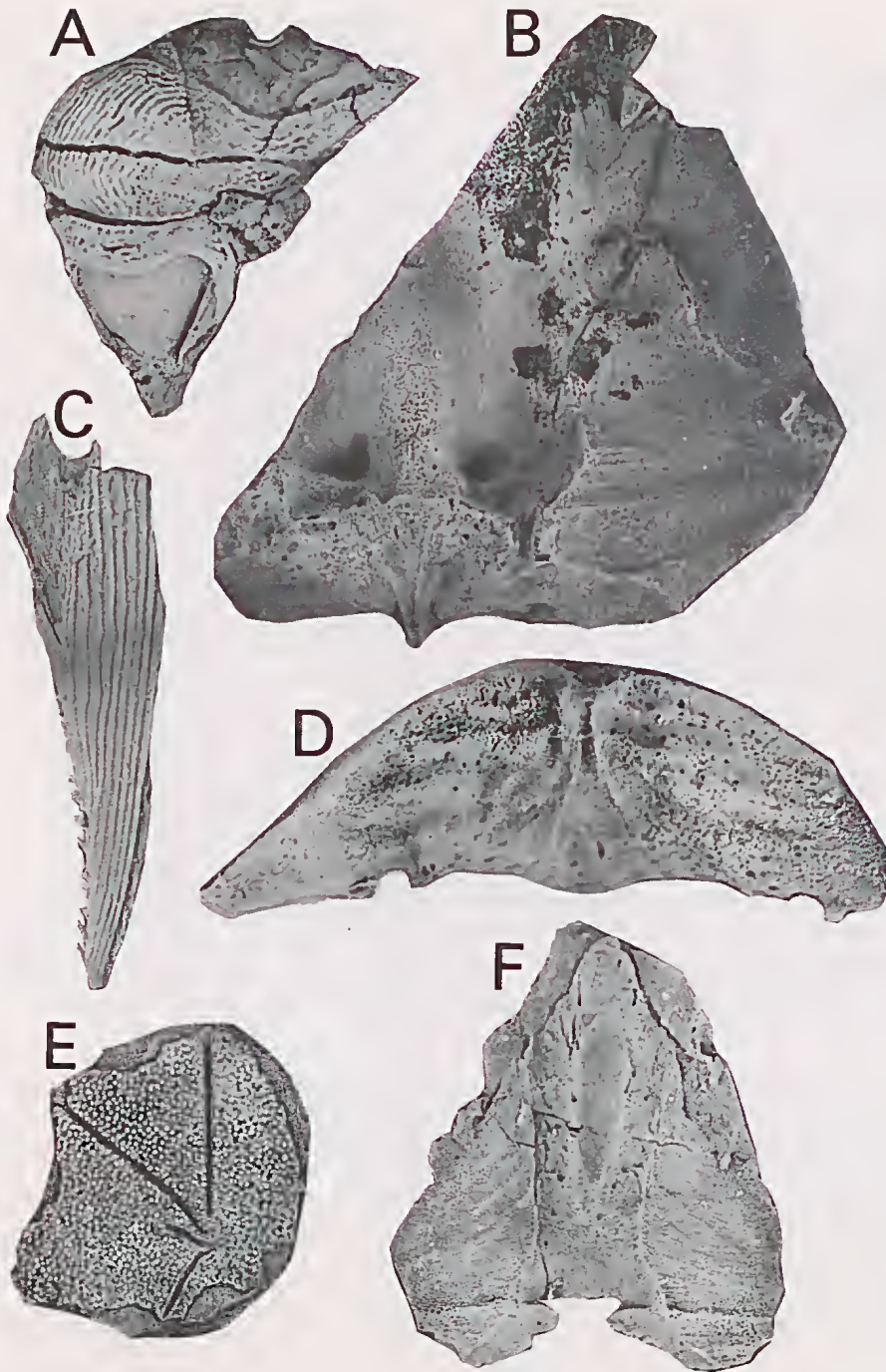


Fig. 4—A, *Errolosteus* cf. *E. goodradigbeensis* Young. Right anterior dorsolateral plate in lateral view, NMVP159894, $\times 1$. B, D, *Taemasosteus maclartiensis* sp. nov., holotype nuchal plate in B, ventral, and D, posterior views, NMVP159887. B, $\times 1$; D, $\times 1.5$. C, *Wijdeaspis warooensis* Young. Left spinal plate in ventral view, NMVP159825, $\times 2$. E, *Taemasosteus* cf. *T. novaustrocambricus*, left central plate in dorsal view, NMVP159889, $\times 1$. F, *Arenipiscis westolli* Young, nuchal plate in ventral view, NMVP159885, $\times 2$. All whitened with ammonium chloride.

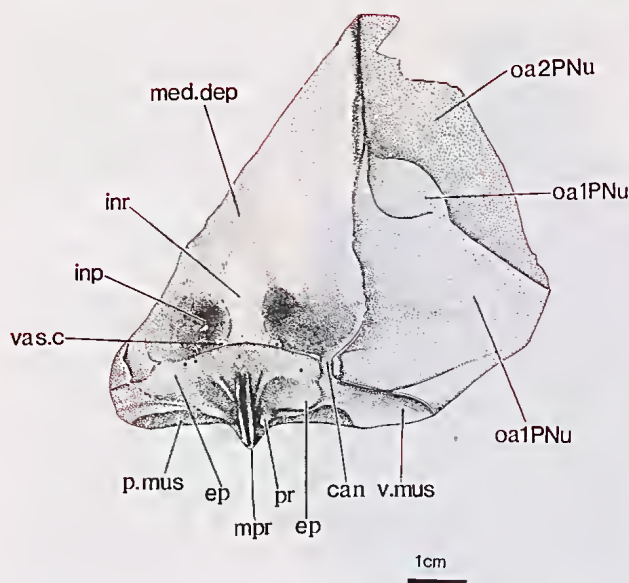


Fig. 5—*Taemasosteus maclartiensis* sp. nov., Emsian, Buchan. Holotype nuchal plate in ventral view, NMVP159887. can, deep grooves between infranuchal pits and ventral muscle area; ep, epiotic prominence; inp, infranuchal pit; inr, infranuchal ridge; med. dep, median depression; mpr, median process or supraoccipital spine; oa1PNu, oa2PNu, overlap areas for paranuchal plate; p.mus, posterior muscle attachment area; vas.c, vascular canals; v.mus, ventral muscle attachment area.

MATERIAL: Holotype NMVP159887 (Figs 4B, D, 5), a large portion of the nuchal plate, showing all of the characteristic features; MUGD6064, an almost complete nuchal plate, more worn than the holotype; NMVP41829, almost complete left paranuchal plate with part of left side of nuchal attached (Fig. 6A); NMVP159891, complete right anterior lateral plate (Fig. 7A, E).

OCCURRENCE: All specimens were collected from the vicinity of the Rocky Camp quarry, on the eastern slope of the hill, in the topmost section of the McLarty Member and lowermost Rocky Camp Member (Fig. 1). Most of the material was collected by the author and friends during 1980-1983.

REMARKS: The material is believed to be conspecific because all these plates show differences from the type species, and were collected from the same stratigraphic horizon. The new species is distinctive in the morphology of the nuchal, paranuchal and anterior lateral plates, and as there are two specimens of the nuchal plate which exhibit distinctive features compared to *T. novaustrocambricus* of the same size, the differences between the type species and *T. maclartiensis* sp. nov. are unlikely to be due to abnormality or changes during growth.

DESCRIPTION: Nuchal plate. NMVP159887 shows the posterior half of the plate perfectly preserved whereas MUGD6064 gives an overall estimation of proportions of the entire plate. Proportions are similar to *T.*

novaustrocambricus but the posterior margin is straight and the posterior profile of the plate is lower. White (1978, p. 186) noted that in *T. novaustrocambricus* the occipital region of the nuchal plate is raised strongly, more so in larger plates. Examination of the British Museum specimens confirmed that this is a feature of all specimens, and as the occipital region of the nuchal is not strongly elevated in the two specimens from Buchan it is assumed to be a specific characteristic of *T. novaustrocambricus*. The middle part of the posterior margin of the nuchal in *T. maclartiensis* (Fig. 5) is only slightly concave, whereas in all specimens of *T. novaustrocambricus* this margin is strongly concave medially (bordering the posterior face, giving the whole of the posterior margin a W-shape seen in Fig. 8A, B). As in the type species the infranuchal pits (inp) are also large and deep in *T. maclartiensis*, being stepped in NMVP159887 with the deepest excavation in the anterior half and the infranuchal ridge (inr) giving way anteriorly to a median depression (med. dep). The posterolateral corner of each infranuchal pit has a clearly marked deep groove (can) leading to the ventromesial corner of the ventral muscle attachment region (v. mus) on the posterior face of the plate. MUGD6064 is very worn in this region but still shows vestiges of the canals. The epiotic prominences (ep) are clearly seen immediately posterior to these canals in the holotype (Fig. 5). The supraoccipital spine (mpr) is a bifid structure with smaller pointed protuberances (pr) flanking each side close to the dorsal margin. Below the supraoccipital spine is a broad concave area, presumably for attachment of the medial division of the levator capituli muscles. Lateral to the epiotic prominences is an extensive, smooth region for other muscle attachment (v. mus), and dorsal to this field on the posterior face of the plate is a posterior muscle attachment area (p. mus). White (1978) noted the presence of foramina for the posterior cerebral veins around the supraoccipital spine on the nuchal plate of *T. novaustrocambricus*. In the holotype of *T. maclartiensis* there are numerous small pores in this region (vas. c), presumably for vascular supply, but large conspicuous foramina are not present. The dorsal smooth overlap flange for the extrascapular plates appears to be more extensive for the holotype of *T. maclartiensis* than for any of the figured specimens of *T. novaustrocambricus*, but such differences are difficult to define as specific characters. As in the type species there are two-tiered overlap areas for the paranuchal plates (oa1PNu, oa2PNu). At the junction of the thin anterior overlap lamina with the thicker posterior overlap area on the holotype there is a semicircular median thickening intermediate in height between the two levels (Fig. 8A, oaPNu).

The paranuchal plate is well preserved on NMVP41829 (Fig. 6A), where it is articulated to part of the nuchal plate, missing only the posteromesial corner. This specimen differs from the paranuchal plates of *T. novaustrocambricus* in having a straight posterior margin (pm) which forms an angle of 50° from the suture with the nuchal plate. All the figured paranuchal

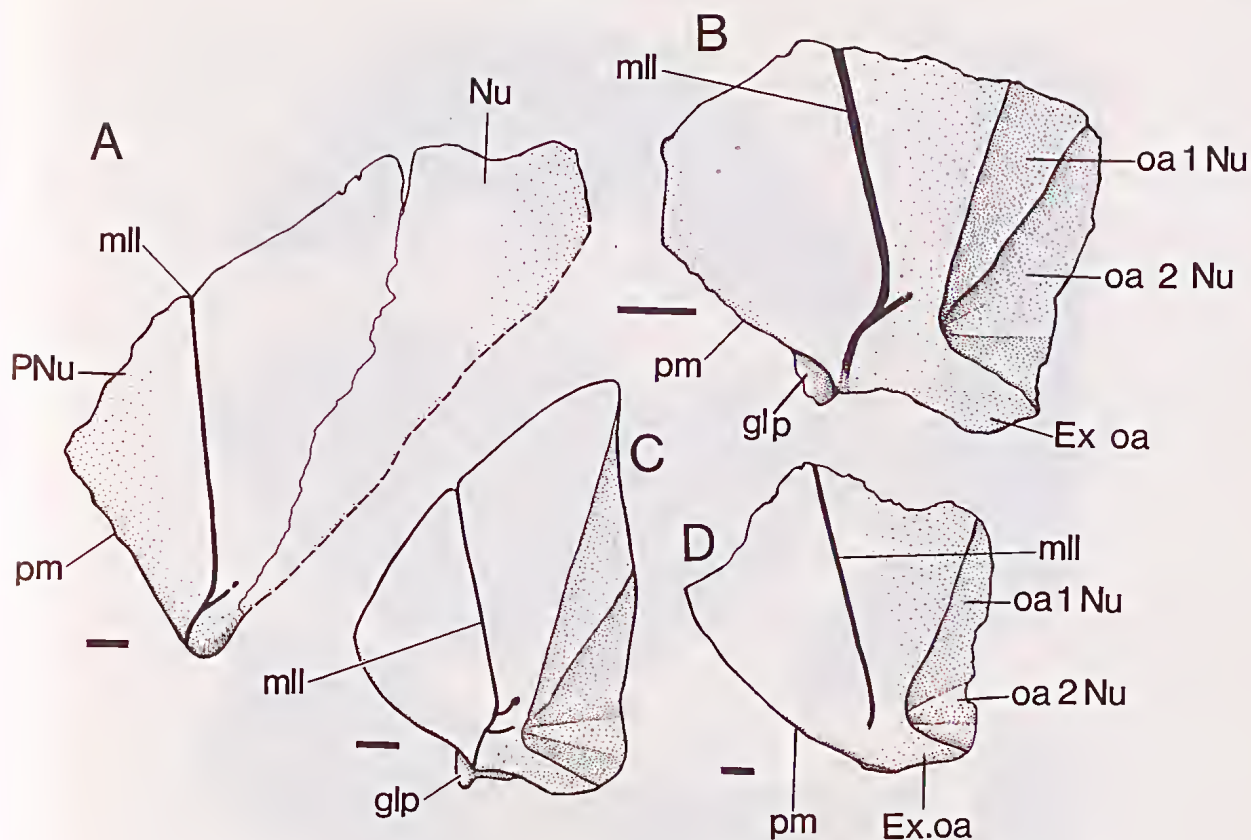


Fig. 6—*Taemasosteus* paranuchal plates in dorsal view. A, *T. maclartiensis* NMVP41829, Buchan. B-D, *T. novaustrocambricus*. B, NMVP159886, Buchan. C, restoration of paranuchal plate by White (1978, fig. 77, reversed to match other plates figured here). D, British Museum specimen P33712, *Taemas*, from White (1978, pl. 9C). Bar scale equals one centimetre. Ex. oa, area overlain by extrascapular plates; glp, glenoid process; mll, main lateral line canal groove; Nu, nuchal plate; oa1Nu, oa2Nu, areas overlapped by nuchal plate; pm, posterior margin of paranuchal plate; PNu, paranuchal plate.

plates of *T. novaustrocambricus* have convex posterior margins and make an angle close to 65° with the external contact margin of the nuchal plate (White 1978, pl. 9A, C, D; Fig. 6 B, C, D). The course of the main lateral line canal (mll) is essentially as in the type species.

The anterior lateral plate of *T. maclartiensis* (Fig. 7A, E) differs from that of the type species in having a smaller number of toothed ridges on the apronic lamina. In the figured specimens of *T. novaustrocambricus* (White 1978) and in CPC25337 there are 7-10 toothed ridges on the apron, whereas the Buchan specimen shows only 4. As the best preserved specimen of this plate of *T. novaustrocambricus* (White 1978, pl. 12A) is approximately the same size as the Buchan specimen these differences cannot be attributed to growth changes and are here regarded as specific features. Another difference between the species is that the apronic lamina is strongly inturned on *T. maclartiensis*, forming an angle of 65° to the lateral lamina of the trunkshield, compared to 44° for that of the type species, as measured on CPC25337.

EUARTHRODIRA gen. indet.

MATERIAL: NMVP159890, an almost complete left suborbital plate (Fig. 7F) from the base of the Rocky Camp Member, Murrindal Limestone, Buchan Group, on the eastern slope of Rocky Camp Hill (Fig. 1).

REMARKS: This large specimen bears very little dermal ornament which is concentrated close to the centre of radiation of the plate, and these are of low rounded tubercles. There is no orbital notch present, but there is a well developed linguiform process for attachment of the autopalatine. This feature is characteristic of higher brachythoracids (Dennis & Miles 1983, Young 1981b), being absent on forms such as *Holonema* (Miles 1971), *Buchanosteus* and *Goodradigbeon* (Young 1979, White 1978). The figured suborbital plates of *Taemasosteus novaustrocambricus* (White 1978) differ in having an orbital notch, but are otherwise similar to this specimen (except that the presence of a linguiform process is not known). In the absence of features linking this plate to any of the recorded brachythoracids from Buchan or

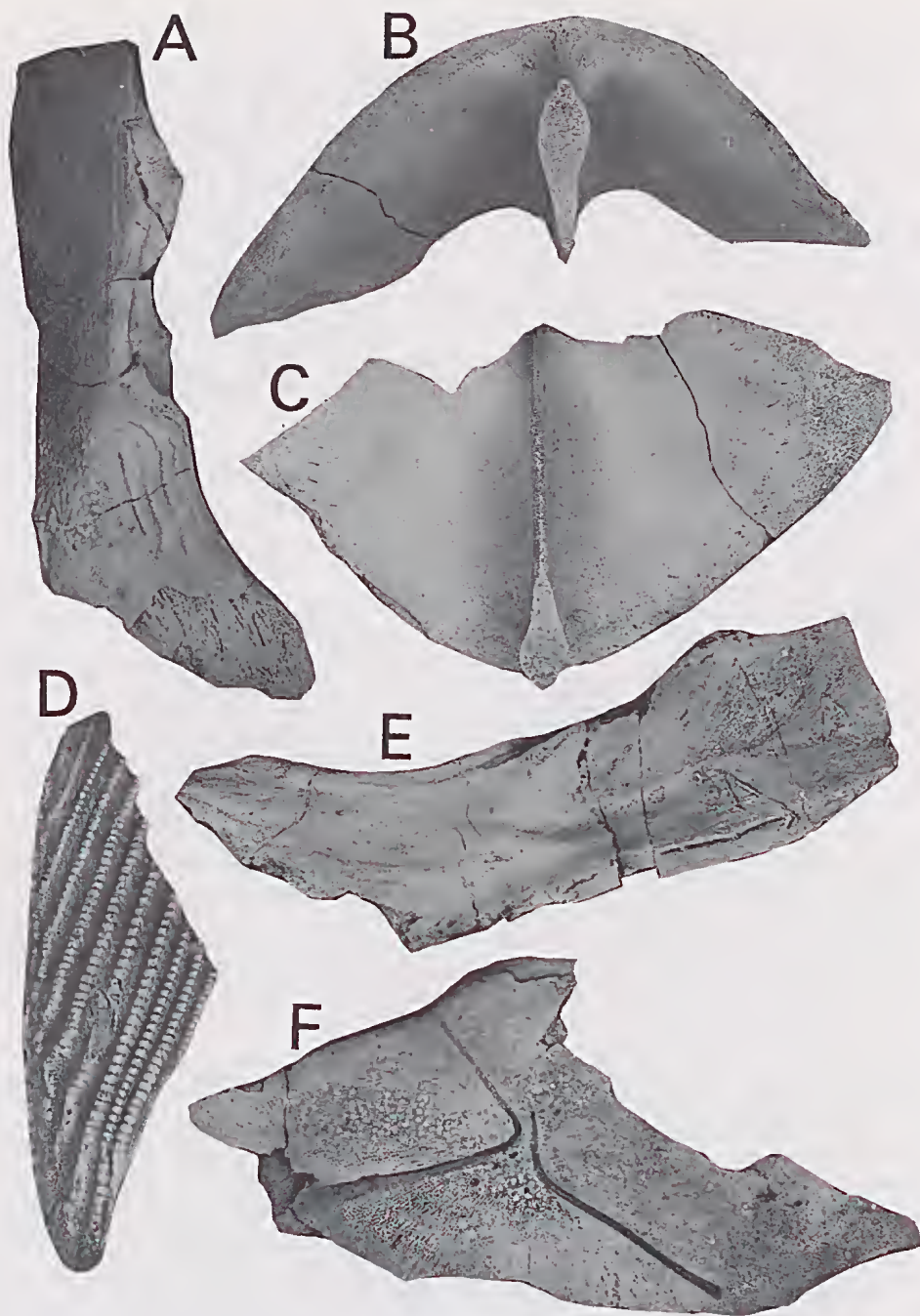
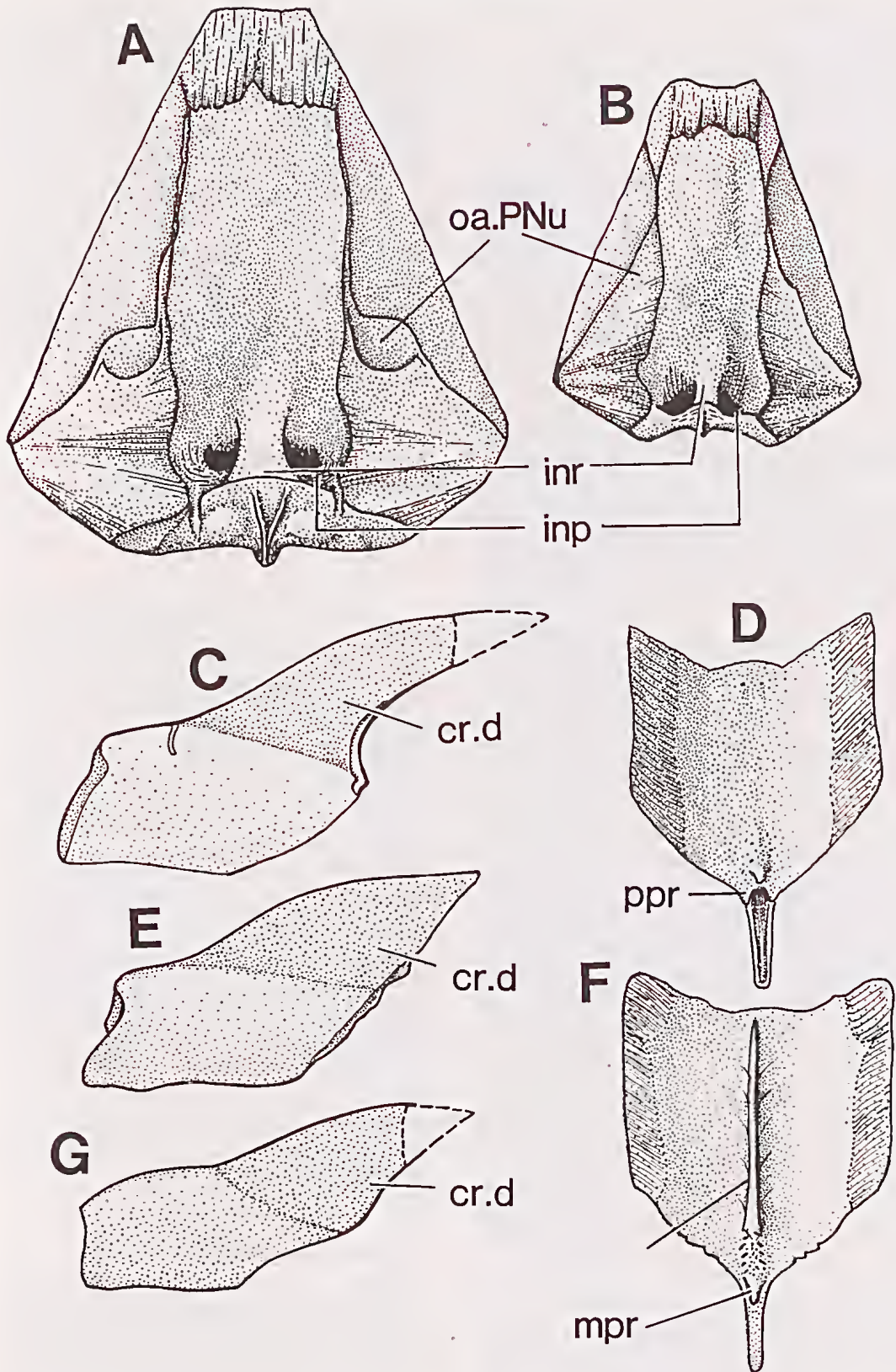


Fig. 7—A, E, *Taemasosteus maclartiensis* sp. nov., right anterior lateral plate in A, anterior, and E, mesial views, NMVP159891, $\times 1$. B, C, D, *Taemasosteus* cf. *T. novaustrocambricus*. B, C, median dorsal plate in B, posterior and C, ventral views, NMVP159888, $\times 0.8$. D, right interolateral plate, NMVP161865 in anterior view, $\times 1.5$. F, Brachythoracid euarthrodire, genus indeterminate, left sub-orbital plate in lateral view, NMVP159890, $\times 1$. All whitened with ammonium chloride.

Fig. 8—Comparison between A, *Taemasosteus maclartiensis* and B, *T. novaustrocambricus* nuchal plates in ventral view. A, restoration based on holotype, NMVP159887, B, from White (1978, fig. 78). C-F, comparison between palaeacanthaspoid median dorsal plates in left lateral (C, E, G) and ventral (D, F) views. C, D, *Murrindalaspis wallacei* gen. et sp. nov. E, F, *Weejasperaspis gavini*. G, *Palaeacanthaspis vasta*. E, F, G from White (1978, figs 12, 15, 19). cr.d, medial dorsal crest; inp, infranuchal pit; inr, infranuchal ridge; mpr, median ventral process; oa, PNu, area overlapped by paranuchal plate; ppr, paved posterior processes at base of crest; vk, median ventral keel.



Taemas 1 refer this suborbital plate to indeterminate Euarthrodira.

DISCUSSION

SOME COMMENTS ON PHYLOGENETIC POSITIONS OF PLACODERMS FROM BUCHAN

The phylogenetic position of the placoderms *Buchanosteus*, *Arenipiscis*, *Errolosteus* and *Taemasosteus* has been thoroughly discussed by Young (1979, 1981b, with further comments on *Buchanosteus* by Denison (1978), Dennis-Bryan & Miles (1983), and White (1978), and on *Taemasosteus* by White (1978) and Denison (1978). Young concluded that these euarthrodirids are primitive phlyctaenaspids relative to the well known coccosteomorphs and higher groups such as pachyosteomorphs. *Taemasosteus* is regarded as the most specialized of the Buchan/Taemas euarthrodirids by virtue of the shortened trunkshield, and may be the sister taxon to *Tityosteus* from the Lower Devonian Rhineland fauna of Germany (Gross 1960). *T. maclartiensis* is undoubtedly a sister species to *T. novaustrocambricus* and does not share any extra features with *Tityosteus* to indicate otherwise.

Murrindalaspis is a palaeacanthaspidoid (*sensu* Miles & Young 1977) known only from the median dorsal plate. Of the palaeacanthaspidoids in which this plate is known (*Dowbrowlania*, *Kinaspis*, *Kosoraspis*, *Palaeacanthaspis* & *Radotina* Denison 1978, *Weejasperaspis* White 1978) only *Palaeacanthaspis* and *Weejasperaspis* possess a well-developed high median dorsal crest comparable to that in *M. wallacei*, although both *Kosoraspis* and *Radotina* possess small median crests similar to *M. bairdi* (Stensiö 1969, Westoll 1967). Three characters can be utilized in an hypothesis of relationships based upon the median dorsal plate of palaeacanthaspidoids: development of the median dorsal crest, development of a median ventral ridge, and the complexity of the ornamentation. All placoderms primitively possess a simple tubercular ornamentation (Denison 1978, Janvier & Pan 1982), which may develop into complex linear ridges, reticulate networks or complex ridged tubercles in different lineages. The presence of a complex ornament pattern, of similar organization, between *Murrindalaspis* and *Weejasperaspis*, taken with their overall similar shape and proportions suggests a close relationship between these genera. Although median dorsal crests have been independently developed in different lineages of placoderms (*Wuttagoonaspis* Ritchie 1973, groenlandaspids Ritchie 1975, *Byssacanthus* Denison 1978, *Bothriolepis cullodenensis* Long 1983a) and may generally be attributed to similar function (homoplasy), the ornament patterns are rarely very similar in different groups, except for primitive groups which share a plesiomorphic dermal ornament (e.g. actinolepidoids and yunnanolepidoid antiarchs) or broadly similar patterns (e.g. phyllolepidids, *Wuttagoonaspis*, *Holonema*). The ventral keel of *Weejasperaspis* is interpreted as a specialization, presumably for articulation of an intermyotomal submedian dorsal plate, as in higher euarthrodirids. The ventral keel is

primitively absent in placoderms (Miles & Dennis 1979, Young 1981b, Denison 1978). I conclude that on the similar development of a complex ornament *Murrindalaspis* is the sister taxon of *Weejasperaspis*. Young (1980) has noted the close similarity between the trunkshield of *Weejasperaspis* to *Brindabellaspis*, commenting that they are probably closely related. Until more remains of *Murrindalaspis* are found it will be unknown whether this genus is more closely related to *Brindabellaspis* than to *Weejasperaspis*.

COMPARISON OF THE ICHTHYOFAUNA FROM BUCHAN

The ichthyofauna from the Buchan Group closely resembles that of the contemporaneous Murrumbidgee Group, New South Wales. Both faunas contain the following taxa, most being endemic to southeastern Australia:

PLACODERM1

Euarthrodira

Brachythoracid phlyctaenaspids

Buchanosteus confertituberculatus, *Arenipiscis westolli*, *Errolosteus goodradigbeensis*, *Taemasosteus novaustrocambricus*.

Petalichthyomorpha

Wijdeaspis warrooensis

In addition the palaeacanthaspidoids from both faunas are closely related forms (*Murrindalaspis* and *Weejasperaspis*), and appear to represent the youngest members of this group worldwide (with *Brindabellaspis* Young 1980) as almost all other palaeacanthaspidoids are described from Gedinian or Siegenian deposits (Denison 1978). The petalichthyid *Wijdeaspis* is also known from the Middle Devonian of Spitsbergen and Severnaya Zemlya (Young 1978), so its Australian occurrence appears to be slightly older (Emsian). The lungfish *Dipnorhynchus* occurs at Buchan and in the Taemas/Wee Jasper faunas, as well as in the Lick Hole Limestone near Kiandra (Campbell & Barwick 1982). The German occurrence of *Dipnorhynchus leunanni* (Lehman & Westoll 1952) from the Rhineland faunas has been commented on by Campbell & Barwick (1983) as probably referable to the Australian genus *Speonesydrion*, making *Dipnorhynchus* an endemic Australian genus. The fish faunas from the Lower Devonian of Australia contain mostly endemic genera which has led Young (1981a) to suggest that East Gondwana formed an endemic province in the Early Devonian. More systematic description of Australian Early Devonian fish fossils is necessary before detailed comparisons with Northern Hemisphere fish faunas can be evaluated fully.

ACKNOWLEDGEMENTS

Sincere thanks to Dr. Gavin Young, Bureau of Mineral Resources, Canberra, for helpful discussions on the placoderm fossils from Buchan and access to collections of Taemas placoderms in the BMR, and to Peter Forey and Colin Patterson, British Museum of Natural History, London, for allowing me to study the

placoderms from Taemas housed in the British Museum. Dr. Gavin Young and Prof. Ken Campbell are thanked for critically reviewing the manuscript. I would also like to thank the many people who helped collect specimens from Buchan, for without their enthusiasm this paper could not have eventuated: Drs. E. Fordyce, D. Holloway and P. Jell; Mr. M. Wallace, R. Baird, B. Munro, R. Brown, K. Simpson, Miss J. Dowling, Miss K. Orth and Mrs. D. Long. Dr. T. Rich, and Ms. E. Thompson, Museum of Victoria, were most helpful in allowing me to work with the collections of the Museum of Victoria, and Mr G. Quick, Melbourne University, permitted loan of Melbourne University specimens. This work was carried out under tenure of a Rothmans Postdoctoral Fellowship at the Australian National University.

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ORDOVICIAN NAUTILOIDS OF TASMANIA — GOULDOCERATIDAE FAM. NOV. (DISCOSORIDA)

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ABSTRACT: The Middle to Upper Ordovician Benjamin Limestone in Tasmania contains eight genera belonging to the Gouldoceratidae fam. nov. (Discosorida). They are *Gouldoceras synchronena*, *G. obliquum*, *G. benjaminense* sp. nov., *Tasmanoceras zeehanense*, *T. pagei* sp. nov., *Benjaminoceras lauriei* gen. et sp. nov., *Westfieldoceras taylori* gen. et sp. nov., *Paramadiganella banksi* gen. et sp. nov., Gouldoceratidae gen. nov. A, gen. nov. B and gen. nov. C. The Gouldoceratidae are characterised by having expanded siphuncles, cyrtchoanitic to orthochoanitic septal necks, well developed finely laminated endocones, unexpanded bullettes and two layered connecting rings. *Madiganella* from the Late Canadian to Whiterock Horn Valley Siltstone in central Australia also belongs to the Gouldoceratidae.

The endocones in the Gouldoceratidae are composed of very fine layers which mimic the shape of the siphuncle, they have radial crystal growth normal to the connecting rings in both dorsoventral and transverse sections. This suggests that they were deposited as a series of needles by the epithelium of the siphon. It is probable that these deposits were porous and allowed exchange of liquid between the siphon and camerac.

The Gouldoceratidae can be divided into two groups, one has relatively larger siphuncles with orthochoanitic septal necks and easily observed endocones, while the other has cyrtchoanitic septal necks, smaller siphuncle and less well developed endocones.

The Gouldoceratidae are the dominant group of nautiloids in the Ordovician of Tasmania, where they are confined to the Benjamin Limestone and largely to the sequences in the Florentine Valley (Figs 1-4). Only *Gouldoceras* and *Tasmanoceras* have been found elsewhere in Tasmania at localities indicated on Fig. 1. The earliest member of the family is *Madiganella* from central Australia. Unfortunately there is a long time break between its Late Canadian-Early Whiterock occurrences in central Australia and the Late Chazy-Early Blackriver age of the oldest gouldoceratid in Tasmania. The course of evolution in the Gouldoceratidae is uncertain due to this major break and other major gaps in the Upper Limestone Member of the Benjamin Limestone.

The Palaeozoic sequence in Tasmania can be divided into three groups; the dominantly clastic Denison Group, the carbonate Gordon Group and the clastic Eldon Group (Burrett *et al.* 1984). These groups range in age from Middle Cambrian to Devonian. The nautiloid faunas are mainly from the Gordon Group. The few specimens known from the Denison or Eldon Groups are too poorly preserved to allow a detailed examination (Stait 1983). The Gordon Group is composed of three formations and ranges in age from Upper Canadian to Maysville (mid-Arenig to Ashgill). The basal formation is the Karmberg Limestone which is overlain by the Cashions Creek Limestone and this is overlain by the Benjamin Limestone. The Benjamin Limestone is subdivided into three members (Fig. 5). The basal member is the Lower Limestone Member, which is overlain by the Lord's Siltstone Member and this is overlain by the Upper Limestone Member (Corbett & Banks 1974, Webby *et al.* 1981, Burrett *et al.* 1984). The Benjamin Limestone is dominantly peritidal, with most of the se-

quence consisting of intertidal carbonates. The nautiloids are largely confined to the small number of shallow subtidal beds and to the tidal channels within the intertidal sediments. The high energy environment in which the nautiloids were deposited has meant that the majority of the specimens are broken with only the solid calcite endosiphuncles preserved. This is especially true of *Tasmanoceras*, where the heavily calcified endosiphuncles are often found in large numbers, all current oriented, in tidal channels.

More detailed discussion of the stratigraphy and geologic setting of the Gordon Group can be found in Corbett and Banks 1974, Webby *et al.* 1981 and Burrett *et al.* 1984.

PREVIOUS STUDIES

The first descriptions of nautiloid faunas from Tasmania were by Etheridge (1883) and Johnston (1888). There was no further work published on the nautiloids until Teichert (1947) described an endocerid fauna from Adamsfield. Teichert and Glenister (1952), in their description of the Australian nautiloid faunas, established *Tasmanoceras* and *Hecatoceras* from Tasmania. Teichert and Glenister (1953) described a large fauna of Ordovician nautiloids from Tasmania. Recently Stait has undertaken a more complete examination of the faunas from carefully measured sections in an attempt to place the nautiloid ranges in a biostratigraphic framework. Stait (1980) erected *Gouldoceras*, and revised *Hecatoceras* Teichert & Glenister. The other fauna from Tasmania is either published or in the process of being published, and includes Stait (1982) on the oncocerids, Stait (1983) on the tarphycerids and ellesmerocerids, Stait (in press) on the



Fig. 1—Locality map of Tasmania, indicating the areas collected in this study. A more detailed map of the Florentine Valley is given in Figure 2.

actinocerids and Stait and Flower (in press) on the michelinocerids. Description of the endocerids is in progress and it is hoped that the study will soon be completed; unpublished data from this projected study are used in the following section.

AGE AND CORRELATION

A family consisting largely of endemic genera rarely has utility for international correlation but it is hoped that now the Gouldoceratidae have been described specimens will be found in other areas.

The coexisting nautiloids are generally long-ranging, widespread forms such as *Discoceras* and *Gorbyoceras*, or endemic forms such as *Hecatoceras* and *Gordonoceras*, and therefore are also difficult to use in international correlation.

Correlation within Tasmania is possible using the nautiloid faunas. The generally small number of specimens available makes it impossible to obtain zonal boundaries for a formal biostratigraphy, instead six broad generic assemblages are delimited. These assemblages in ascending order are:

1. *Piloceras*—*Manchuroceras* assemblage which consists of *Manchuroceras*, *Piloceras*, *Manchuroceratidae* gen. nov., *Yehlioceras*, *Allocotoceras* and *Pynoceras*.

2. *Wutinoceras*—*Adamsoceras* assemblage which contains *Wutinoceras*, *Adamsoceras* and *Chaohuceras*.

3. *Discoceras*—*Gorbyoceras* assemblage which contains *Discoceras*, *Gorbyoceras*, *Mysterioceras*, *Paramadiganella*, *Gouldoceratidae* gen. nov. A, *Actinocerida*

gen. nov., *Michelinocerida* gen. nov., *Orthoceras*, *Beloitoceras*, *Centrocyrtoceras*, *Armenoceras* and three new genera of endocerids.

4. *Tasmanoceras*—*Hecatoceras*—*Gouldoceras* assemblage which consists of *Tasmanoceras*, *Hecatoceras*, *Gouldoceras*, *Anaspyroceras*, *Discoceras*, *Beloitoceras*, *Miamoceras* and *Zeehanoceras*.

5. *Gordonoceras* assemblage which contains only *Gordonoceras*.

6. *Westfieldoceras* assemblage which contains *Westfieldoceras*, *Gouldoceratidae* gen. nov. B, *Gouldoceratidae* gen. nov. C, *Augustoceras* and ?*Armenoceras*.

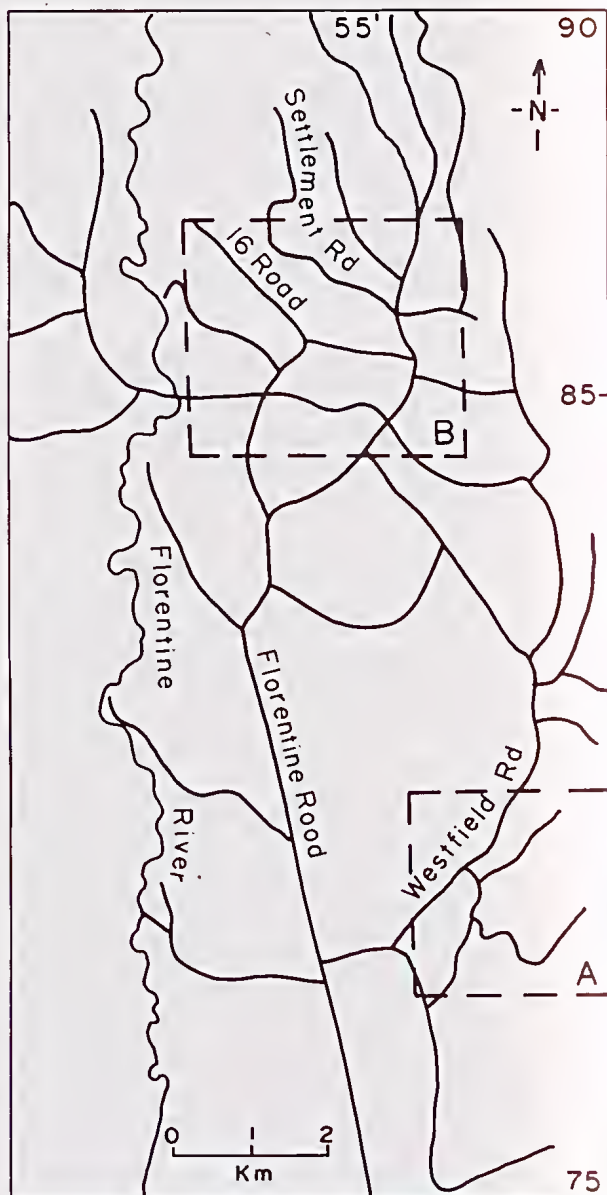


Fig. 2—Map of the Florentine Valley, A and B indicate the location of the inserts shown in Figures 3 and 4 respectively.

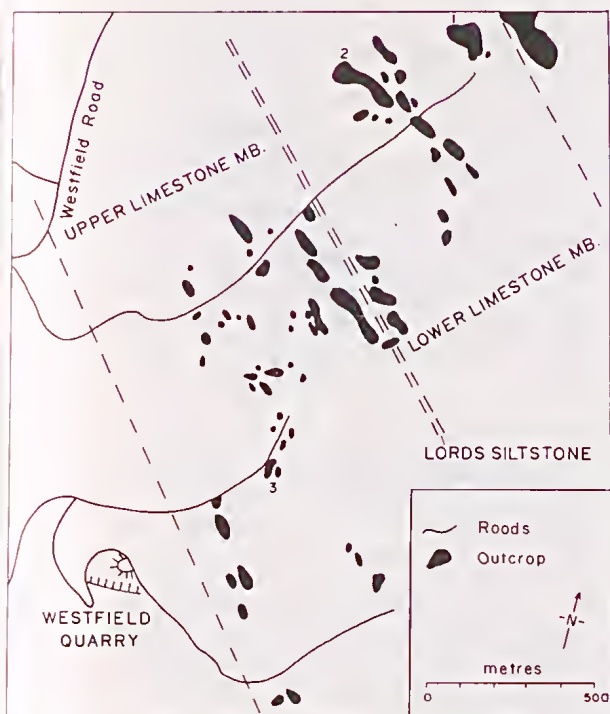


Fig. 3—Map showing the collecting localities at the Westfield section (modified from Calver 1977).

International correlations are made mainly on the basis of the coexisting conodont faunas and a short summary of the ages obtained is included herein for completeness.

Gouldoceratidae gen. nov. A, *Benjaminoceras* and *Paramadiganella* occur near the base of the Lower Limestone Member. Conodonts from this level include *Phragmodus* sp. nov., *Tasmanognathus careyi* and *Chirognathus monodactylus*, tentatively suggesting a correlation with the Blackriveran (C. F. Burrett pers. comm.). *Tasmanoceras* and *Gouldoceras* occur in the middle and upper part of the Lower Limestone Member. The conodonts present are *Phragmodus undatus*, *Bryantodina abrupta*, *Plectodina* cf. *furcata* and *Plectodina aculeata*, suggesting a correlation with faunas 8 and 9 of Sweet and Bergström (1976) (C. F. Burrett pers. comm.). *Westfieldoceras*, Gouldoceratidae gen. nov. B and Gouldoceratidae gen. nov. C occur at the top of the Upper Limestone Member. The conodonts present include *Oulodus robustus*, *O.* cf. *oregonia*, *Plectodina* cf. *furcata* and *Staufferella falcata*. This suggests a correlation with fauna 11 of Sweet and Bergström (1976) (C. F. Burrett pers. comm.).

MORPHOLOGIC TRENDS IN THE GOULDOCERATIDAE

As discussed elsewhere the only non-Tasmanian genus which definitely belongs to the Gouldoceratidae is *Madiganella*. It has thick two-layered connecting rings, unexpanded bullettes, endocones and the siphuncle

changes from amphora shaped to symmetrically expanded and moves relatively towards the venter with growth (Fig. 6). *Madiganella* has recently been redescribed in detail (Stait & Laurie in press) and does not require further discussion here.

As there are only a small number of specimens known and many major gaps in the sequence no serious attempt can be made at a phylogeny for the Gouldoceratidae. However, it is possible to comment on the features which unify the group and apparent trends in morphology through time which may later prove to form an evolutionary sequence.

The Gouldoceratidae are diagnosed below. Their most obvious characters are the finely spicular laminated endocones and the thick two-layered connecting rings. They also all have a siphuncle between the centre and venter and an almost total lack of cameral deposits.

Within this family there are two distinct groupings. These possibly will be designated as subfamilies, when the Gouldoceratidae are better known. The two groups can be distinguished largely on the basis of the amount of expansion of the siphuncular segments, the relative size and position of the siphuncle and the morphology of the septal necks.

The first of these two groups includes Gouldoceratidae gen. nov. A, *Benjaminoceras* and *Tasmanoceras*. It shows trends characterized by a change from cyrtchoanitic to orthochoanitic curvature of the septal necks (Fig. 7), an increase in the relative size of the siphuncle, a more marginal position for the siphuncle and increasing instability in the position of the siphonal space.

The second group consists of *Paramadiganella*, *Gouldoceras*, Gouldoceratidae gen. nov. B and *Westfieldoceras*. This group shows trends in which the

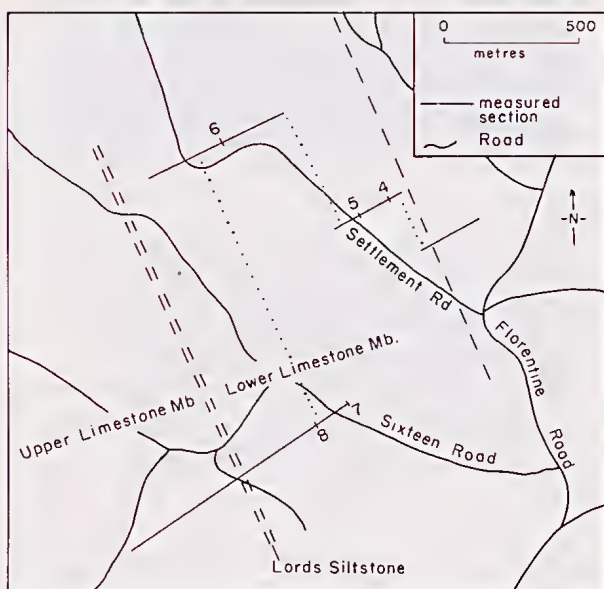


Fig. 4—Map showing the collecting localities at the Settlement Road section.

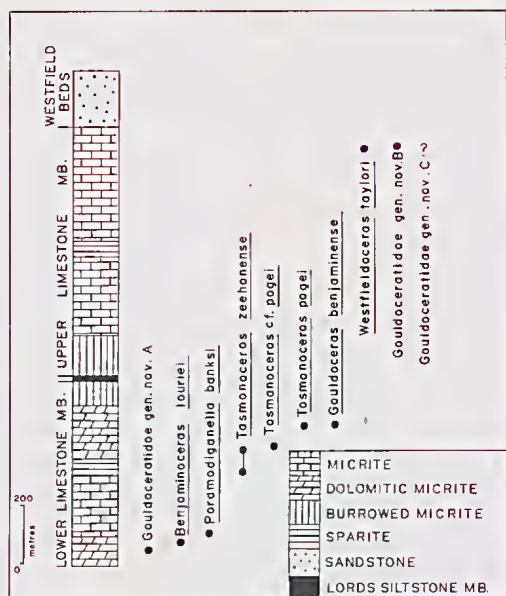


Fig. 5—Composite stratigraphic section of the Benjamin Limestone in the Florentine Valley. Lower Limestone Member based on the Settlement Road Section of Calver (Unpub. data), while the Upper Limestone Member is based on Page (1978).

septal necks become more cyrtchoanitic, the free part of the septa near the septal foramen increasingly bend to point towards the apex (Fig. 7) and the siphuncular segments change slope so that the segments slope adorally from the venter to the dorsum.

In addition the Gouldoceratidae also show a tendency to change the position and shape of the siphuncle with growth (Fig. 14A). This is most noticeable in *Paramadiganella*, *Tasmanoceras* and *Benjaminoceras*. *Madiganella* also shows this change in position and shape of the siphuncle with growth (Stait & Laurie in press).

The shape of the septal necks in the Gouldoceratidae appears to change in a systematic way. These changes are illustrated in Fig. 7. The change from cyrtchoanitic to orthochoanitic septal necks in the first group of the Gouldoceratidae is probably a response to the larger size, more marginal position and less expanded siphuncle in this group (Fig. 7). However, the reason for the complex shape of the septal necks in the younger members of the second group of the Gouldoceratidae (Fig. 7) is not apparent.

Hoeloceras Sweet 1958, from the Middle Ordovician of Norway, was originally placed in the Lambeoceratidae of the Actinocerida. Flower (1976, p. 547) indicated that he considered *Hoeloceras* to be a discosorid belonging to the Ruedemannoceratidae based mainly on the supposed presence of a free siphonal tube. As has been shown with *Buttsoceras* (Flower 1962) and *Madiganella* (Stait & Laurie in press) free siphonal tubes are often a preservational phenomenon and represent the siphonal space within the endocones. In *H. askeri* the siphuncular segments slope adorally from the venter

to the dorsum, the connecting rings, although described as thin by Sweet (1958), appear to be thick in the illustrations. The thickness of the connecting rings in the *Gouldoceratidae* can be deceptive. The connecting rings are sometimes preferentially removed and when siphonal deposits are present a thin ring is suggested. Another problem is that the rings are two layered and the thin dark layer on the siphonal surface can look like the complete connecting ring, with the thicker, light layer on the cameral surface appearing inorganic in origin. The combination of the above features are not restricted to the Gouldoceratidae, but strongly suggest that, with study, *Hoeloceras* may be assignable to this family.

STRUCTURE OF THE SIPHONAL DEPOSITS

A number of specimens obtained during this study have the siphonal deposits preserved in fine detail. Although there are not enough specimens available to allow the detailed examination that would be desirable, such as serial transverse and longitudinal sections, a great deal of information can be obtained. All members of the Gouldoceratidae show the following structures to various degrees; however, they are best illustrated in *Gouldoceras* and *Gouldoceratidae* gen. nov. A and these two genera will be used as the basis for discussion.

In general terms the siphonal deposits are endocones, composed of a large number of fine individual 'cones' which broadly mimic the shape of the siphuncle but are thicker in the expanded part of the segments than in the septal foramina. Each 'cone' is composed of a band of honey-coloured material which is separated from the adjacent 'cones' by a dark line (probably representing a break in deposition of the endocones). The endocones appear to grow by accretion of a new layer on the inside of the 'endosiphococone', this extends the endocones slightly adorally. Each endocone can be

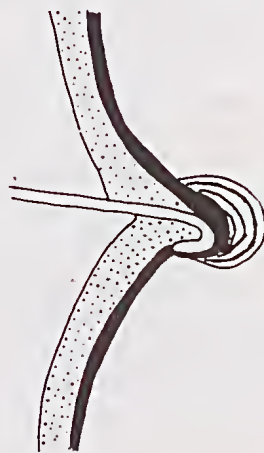


Fig. 6—The septal neck and connecting ring of *Madiganella tatei*, T1255, $\times 15$. Spaced stipple is the siphonal deposits while the close stipple and black areas are the layers of the connecting ring, based on fig. 2L of Stait and Laurie (in press).

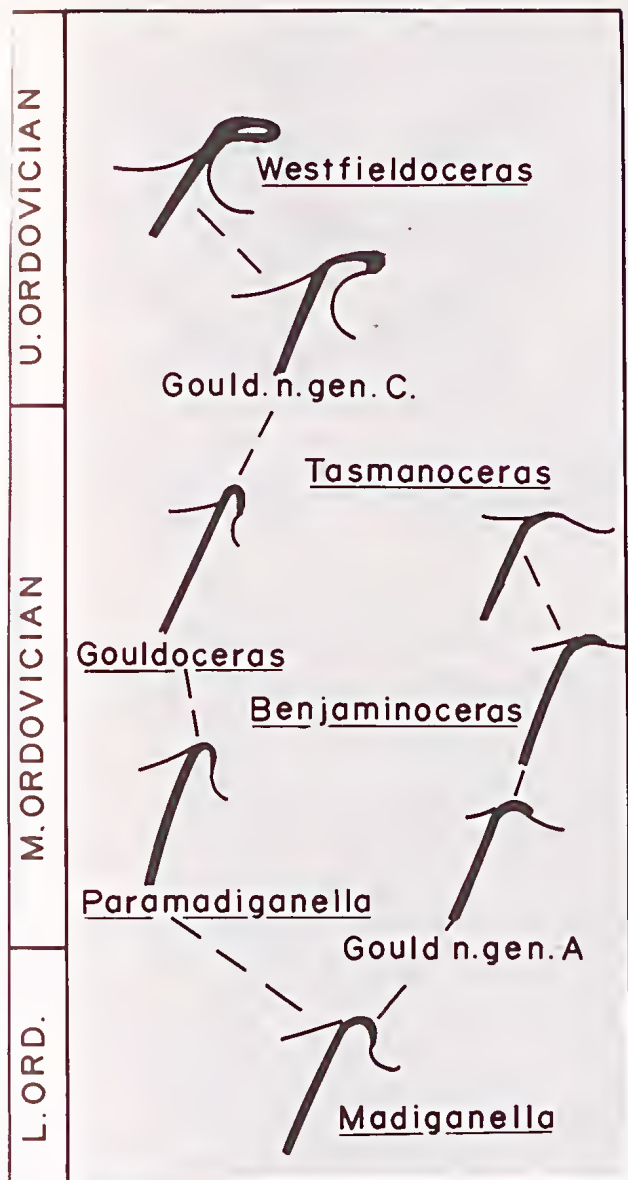


Fig. 7—Shows the variation in the shape of the septal necks within the Gouldoceratidae. The lines are not meant to imply phylogenetic relationships but similar morphologies.

traced from where it meets the connecting ring, adorally, back through the specimen without a break. In *Gouldoceras* the endocones often show a variation in thickness related to the position of the radial spaces in the segments, thus supporting the suggestion as to the function of these spaces (discussed below). In transverse section the endocones show the same continuity and can easily be traced around the siphuncle. The thickness of the endocones often varies from the venter to the dorsum, as is demonstrated by the variable position of the siphonal space.

The siphonal deposits also have fine radial structures, normal to the endocones. They are present in both dorsoventral and transverse sections, suggesting they are needle-like rather than blade-like. The needles are not all continuous from the connecting ring to the centre but instead some terminate while others continue. This is a natural consequence of needles which maintain virtually the same size growing from the perimeter of a spheroid towards the centre. This also holds for the longitudinal section especially as the siphuncular segments are expanded. The needles appear to have areas between them (now filled with milky calcite) which do not show the same structure. This is difficult to explain, but a possible solution is suggested by the adoral part of the holotype of *Gouldoceras* (Fig. 8C). In this specimen there are milky calcite areas within the dark micritic matrix which almost certainly represent the arterial system. How this

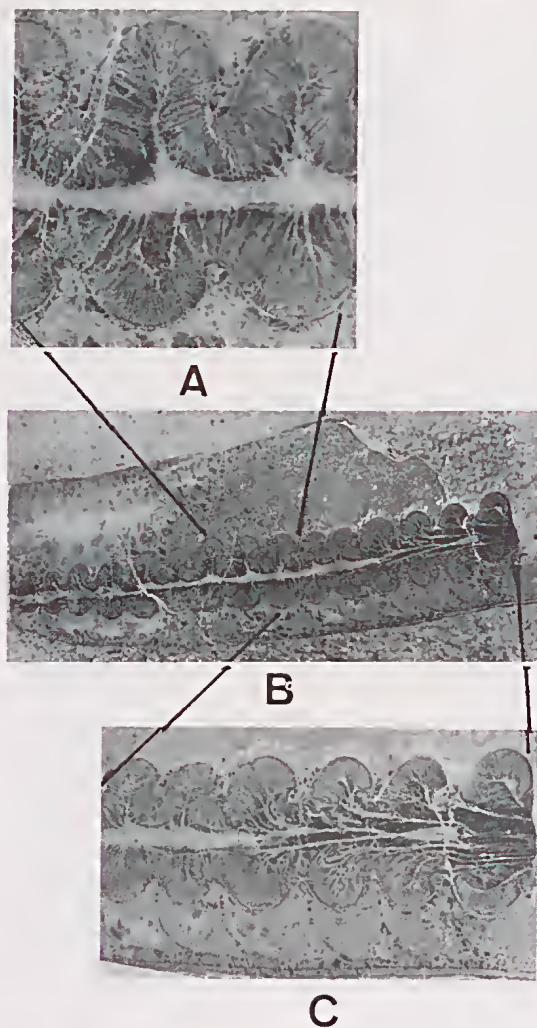


Fig. 8—*Gouldoceras synchronena* UTGD55553. B, sagittal section, $\times 8$. A, an enlargement of the siphuncle showing the siphonal and radial spaces, $\times 2$. C, an enlargement of the orad portion of the siphuncle showing the preserved vascular system, $\times 4$.

could be preserved is open to debate but the most probable explanation is that the arteries were filled with marine waters before the flesh of the siphon rotted and calcite was deposited in these cavities. This may have given the arteries enough strength to be preserved, while the surrounding flesh rotted and was replaced by sediment. Any other series of events would almost certainly have resulted in the destruction of the arterial system. Examination of the arterial system shows that branches enter each siphuncular segment and divide into a very large number of fine 'capillaries' which may have supplied blood to the connecting ring surface. Close examination of the adoral end of UTGD55553 indicates that the siphonal deposits developed around the capillaries, suggesting a continued connection between the siphonal tissue and the camerae (Fig. 8c). I suggest that these capillaries may have maintained connection with the connecting rings even after the endocones became well developed. The needle-like nature of the deposits formed a meshwork, enabling the connections to be maintained with the camerae and allowing the deposition of the necessary siphonal deposits. No information on the method of deposition of the siphonal deposits is obtainable from this material. Although the possibility that it was a series of thin blisters as suggested by Wade (1977a, 1977b) for the georginids cannot be ruled out. Alternately the needles may have grown by addition of material to the inside of the needle which was in direct contact with the epithelium of the siphon.

Other families of discosorids (e.g., Westonoceratidae and Discosoridae) have a similar structure in their siphonal deposits which may represent a similar distributary system. The fine radial structure is also present in the endocones of the Narthecoceratidae and possibly the Troedssonellidae of the Michelinocerida.

How these needle-like structures are related to the blades seen in the actinocerids and endocerids (Teichert & Crick 1974) is a most interesting question, but beyond the scope of this study.

SYSTEMATIC PALAEOLOGY

Terminology used herein follows that of Teichert (1964) and Flower (1964) except for the following: height is any measurement made normal to the axis of the phragmocone in the dorsoventral plane; width is any measurement made normal to the axis of the phragmocone in the lateral plane; siphonal space is the cavity left by the endocones; it probably contained the arterial and venous systems of the animal. (Broadly equivalent to the endosiphontube in endocerids, but the presence of the radial spaces suggests a slightly different structure.); radial space is a cavity formed in the expanded part of the siphuncular segment as the endocones thicken, these spaces are most pronounced in highly expanded segments. Measurements are, wherever feasible, expressed in terms of the siphonal formula of Flower (1968a). All specimens are held in the collections of the Geology Department, University of Tasmania and are prefixed UTGD.

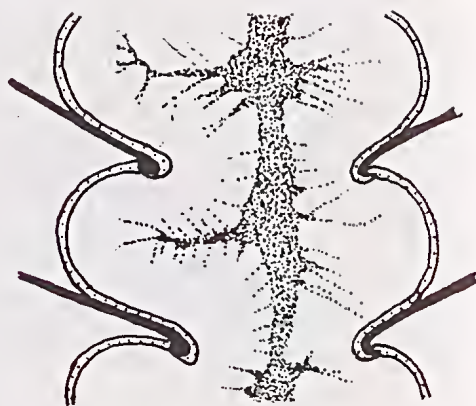


Fig. 9—The siphuncle of *Gouldoceras synchronena*, seventh to ninth segments from the adoral end of UTGD55553, $\times 10$. Stippled area indicates the siphonal and radial spaces.

Order DISCOSORIDA

Family GOULDOCERATIDAE fam. nov.

DIAGNOSIS: Straight to slightly cyrtocoenic, exogastric shells with a circular to slightly depressed cross section. The siphuncle is large from $\frac{1}{4}$ to $\frac{1}{2}$ the diameter of the phragmocone and ventral to central in position. The septal necks range from orthochoanitic to cyrtocoanitic. The siphuncular deposits are composed of thin endocones which leave a central space and in some cases radial spaces. The connecting rings are thick and composed of two layers, with unexpanded bulletpieces.

REMARKS: The Gouldoceratidae are typical of the order Discosorida in the majority of features; however, the connecting rings are simply composed of two layers and do not show the complex differentiation typical of the order. They are similar to those of the Ellesmerocerida, which may suggest that the Gouldoceratidae are a relict group of the ancestral Discosorida, and that they developed from the Ellesmerocerida. However, recent finds in China and Queensland suggest that either the ancestor of the Discosorida is to be found very early in the Ordovician or that the Discosorida are polyphyletic.

Nine genera are herein definitely assigned to the Gouldoceratidae; they are—*Gouldoceras*, *Westfieldoceras*, *Benjaminoceras*, *Paramadiganella*, *Tasmanoceras*, Gouldoceratidae gen. nov. A, Gouldoceratidae gen. nov. B, Gouldoceratidae gen. nov. C. *Madiganella* Teichert & Glenister, from central Australia has recently been examined in detail (Stait & Laurie in press) and clearly belongs to the Gouldoceratidae. The assignment of *Tasmanoceras* to an order or family has been a problem, Teichert and Glenister (1952, p. 739) assigning it to the Endoceratidae of the Endocerida, while Flower (1968b, p. 83) placed it in the Donacoceratinae of the Narthecoceratidae which he transferred to the Michelinocerida. Based on the new material from Tasmania it is clear that *Tasmanoceras* is a member of the Gouldoceratidae of the Discosorida.

While in Nanjing in 1983 Dr Mary Wade of the Queensland Museum and the author observed that the *Pseudowutinoceratidae* Chen & Chen belongs to the *Discosorida* but differs from the *Gouldoceratidae* in having expanded bullettes, well developed cameral deposits and a siphuncle which moves to a dorsal position during growth, although their similarities in size, shape and age give an initial impression of relationship. An undescribed genus of this family occurs in the Georgina Basin, western Queensland (M. Wade pers. comm).

Genus *Gouldoceras* Stait 1980

TYPE SPECIES: *Gouldoceras synchronena* Stait 1980.

REMARKS: When Stait (1980) established *Gouldoceras* he was unable to determine, with any certainty, the thickness of the connecting rings. However, material obtained in the present study indicates that the connecting rings are thick and two layered as in all other members of the *Gouldoceratidae* (Fig. 9). Other than this, the description in Stait (1980) stands.

Gouldoceras benjaminense sp. nov.

Fig. 10A-J

DERIVATION OF NAME: Specimens were collected from the Benjamin Limestone.

MATERIAL: Three isolated siphuncles are known, holotype UTGD121129, and paratypes UTGD121130, 121131 all from the Lower Limestone Member of the Benjamin Limestone at Settlement Road (locality 8 on Fig. 4). The age is Late Blackriver to Early 'Trenton'.

DESCRIPTION: Only isolated siphuncles are known. The siphuncle is slightly curved, probably exogastrically. There are ten siphuncular segments in a length of 25 mm. They are highly expanded and slope adapically from the venter to the dorsum at an angle of 70° to the axis of the siphuncle. Apically on UTGD121129 the siphuncle is 1.0 mm high at the septal foramen, 3.7 mm at the point of maximum expansion and 2.3 mm long, while adorally the corresponding measurements are 1.5 mm, 3.8 mm and 2.3 mm. On the dorsal side of the siphuncle the adapical part of the connecting ring is adnate to the adoral surface of the septum for a distance of 0.8 mm, while ventrally it is adnate for 1.2 mm.

The septal necks are cyrtochoanitic. Adorally the septal necks are 0.4 mm long and the brims are 0.4 mm long on the venter, while the necks are 0.5 mm long, and the brims are 0.4 mm long on the dorsum, apically the corresponding measurements are 0.3 mm, 0.5 mm, 0.4 mm and 0.4 mm. The siphuncular deposits are a continuous lining over the connecting rings and the septal necks. The continuous lining is formed by thin 'endocones' which closely parallel the shape of the siphuncle and fill the siphuncle except for a central space and the radial spaces. There are two short radial spaces in the dorsal part of each siphuncular segment, but only one on the venter. The radial spaces do not penetrate the siphonal deposits. The deposits also have fine radial spicules normal to the connecting rings. The central

space is crossed by lobate structures which are interpreted as diaphragms. The connecting rings are thick and structured. They are two-layered with a thin dark layer on the siphonal surface and a thick lighter layer on the cameral surface.

REMARKS: *G. benjaminense* differs from *Gouldoceras synchronena* in having a higher slope from the venter to the dorsum, diaphragms that cross the central canal and two radial spaces in each segment on the dorsal side of the siphuncle. In the slope of the siphuncular segments *G. benjaminense* is similar to *G. obliquum*, but differs from that species in having two radial spaces on the dorsal side of the siphuncle and in the development of diaphragms across the siphonal space.

Genus *Benjaminoceras* gen. nov.

TYPE SPECIES: *Benjaminoceras lauriei* sp. nov.

DERIVATION OF NAME: The type species was collected from the Benjamin Limestone.

DIAGNOSIS: Phragmocone is a straight, subcircular longicone with venter slightly flattened; siphuncle evenly and moderately expanded; siphuncular deposits thin continuous endocones which are symmetrical dorsoventrally; septal necks orthochoanitic, short; connecting rings thick and composed of two layers; area of adnation with the septa short; no cameral deposits.

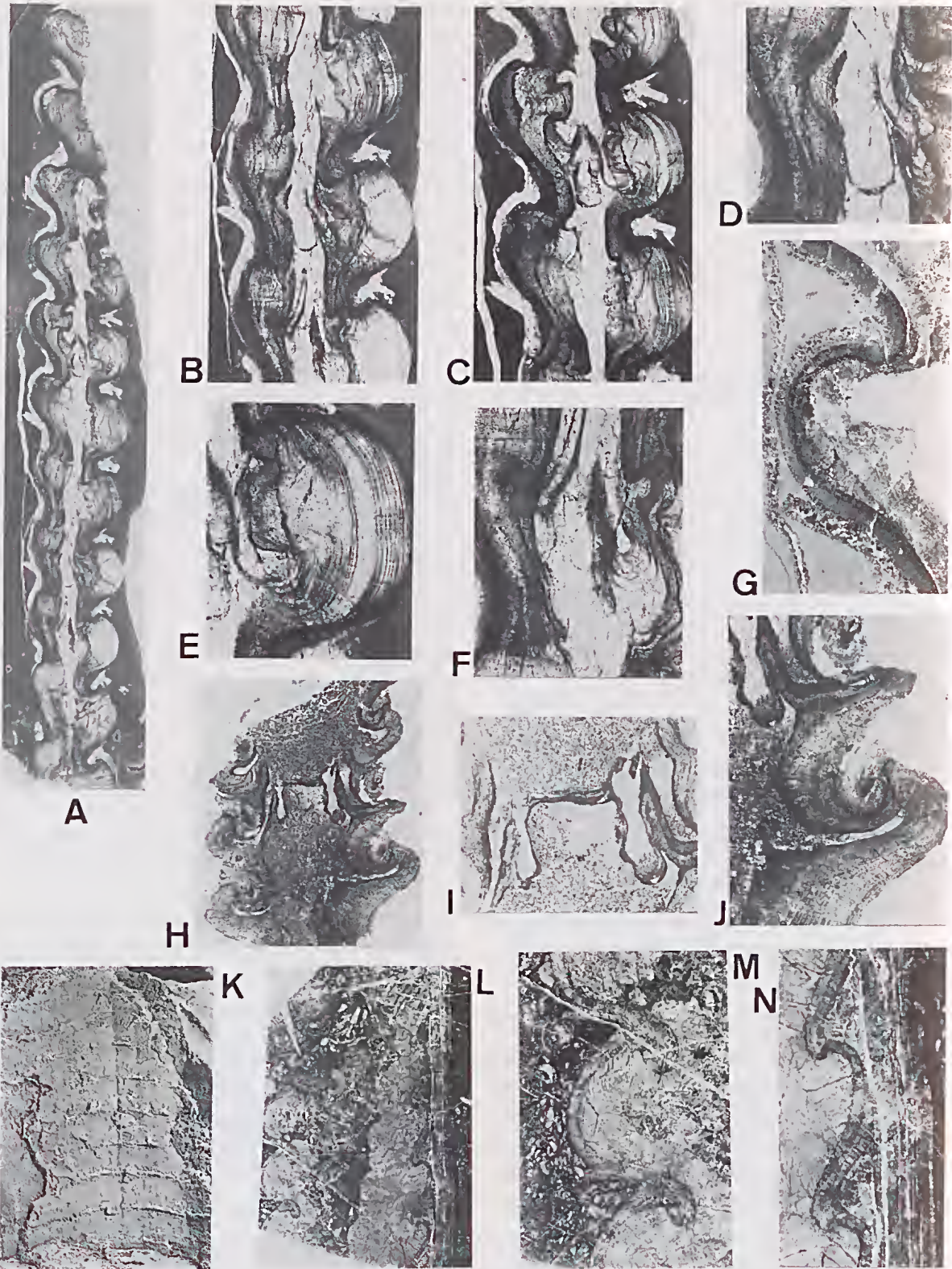
REMARKS: This genus is assignable to the *Gouldoceratidae* as it has thick, two-layered connecting rings and thin well developed endocones. It differs from the other members of this family in having longer, less expanded siphuncular segments and orthochoanitic septal necks.

A specimen collected from the same horizon as *Benjaminoceras lauriei* may represent a more mature growth stage of *Benjaminoceras* (UTGD121134). The only important difference between this specimen and *Benjaminoceras* is the morphology of the septal necks, which exhibit three bends (Fig. 11J). The transition from the simple orthochoanitic septal necks of *Benjaminoceras* to those of UTGD121134 would only require minor changes in morphology. Although the shape of the septal necks in the other members of the *Gouldoceratidae* do not vary markedly during growth, other structures often undergo dramatic morphological change. An example of such a change is the variation in the position of the siphuncle in *Paramadiganella*. Considering the potential variability of the *Gouldoceratidae* and the lack of more complete material the specimen is tentatively assigned to *Benjaminoceras lauriei*. The size of UTGD121134, nearly twice that of any definite *Benjaminoceras* specimen, is consistent with this interpretation.

Benjaminoceras lauriei sp. nov.

Figs 11, 12, 13

DERIVATION OF NAME: For Dr. J. R. Laurie who helped collect many of the nautiloids described herein.



MATERIAL: Five partially complete phragmocones; holotype UTGD121132, paratypes UTGD121133, 121135 and 121136, other material UTGD121134 all from the Lower Limestone Member of the Benjamin Limestone (locality 5 on Fig. 4). The age is Blackriver.

DESCRIPTION: The body chamber is unknown. The phragmocone is a slowly expanding orthoconic longicone, subcircular in cross section, with the venter slightly flattened. The holotype consists of 16 segments in a distance of 40 mm. The siphuncle is one-third of the diameter of the phragmocone. The siphuncular segments are moderately and evenly expanded, with the expanded part in contact with the ventral phragmocone wall for a short distance. The siphuncular segments slope apicad from the venter to the dorsum at 80°. The septa are gently curved with the point of maximum depth at the siphuncle. The connecting rings are adnate to both the adapical and adoral sides of the septa for a short distance, 0.1 mm.

The siphonal formula is 1.6/3.1/-:1.1/4.2/-;2.3 adorally, while at the most adapical segment it is 1.3/2.6/-:0.9/3.6/-;1.9.

The septal necks are orthochoanitic and moderately long, 0.6 mm on the dorsum and 0.4 mm on the venter; the corresponding adapical measurements are 0.4 mm and 0.2 mm. The siphuncle contains extensive and well developed deposits, but the original structures are masked by recrystallization in the known specimens. Enough of the deposits are preserved to indicate that they were finely laminated continuous cones which converge apically at a low angle. The surface of these cones is wavy, mimicking the shape of the siphuncular segments. A central space was probably present although only the adoral portion is now preserved (Fig. 11A). The deposits extend adorally for the same distance both on the venter and the dorsum. The connecting rings are thick and layered. There are two distinct layers: 1, a thin black layer on the siphonal surface and 2, a thick lighter layer on the cameral surface. A light band is sometimes preserved at the oral end of the connecting ring between the light and the dark layer on the siphonal surface. This light band lenses out apically along the connecting ring and is not known to reach the next septal foramen. There are no cameral deposits known.

REMARKS: See generic remarks.

Genus *Paramadiganella* gen. nov.

TYPE SPECIES: *Paramadiganella banksi* sp. nov.

DIAGNOSIS: Phragmocone subcircular, orthoconic longicone, with the venter slightly flattened; siphuncle small, variable in position but always between the centre and venter and never in contact with the ventral phragmocone wall; siphuncular segments highly expanded with the adoral segments more expanded; in the adapical portion of the phragmocone the segments slope adorally from the venter to the dorsum, while adorally the segments are normal to the siphuncular axis; septal necks and brims are short and cyrtchoanitic; there are siphuncular deposits present in the adapical asymmetric segments; these are parietal deposits which grow apically to form endocones; in the adoral symmetrical segments there are no demonstrable deposits; connecting rings are thick and consist of two layers, a thin dark layer on the siphonal surface and a thick lighter layer on the cameral surface; connecting rings not adnate to the septa; both hyposeptal and episeptal deposits present, but only poorly developed; conch wall is composed of three layers.

REMARKS: *Paramadiganella* is unusual as the siphuncle changes position within the phragmocone, and after this change both the form and the nature of the internal deposits are dramatically altered. The presence of the thick, two-layered connecting rings and the endocone-like deposits indicate that *Paramadiganella* is a typical member of the Gouldoceratidae, but with the change in position of the siphuncle and the presence of cameral deposits is different to any other members of this family. The adoral segments of *Paramadiganella* are very similar to those of *Madiganella* in the shape of the siphuncle and the presence of the endocone-like siphonal deposits, but the genera differ in the size and position of the siphuncle and in the curvature of the septa.

Paramadiganella banksi sp. nov.

Fig. 14

MATERIAL: Ten partially preserved phragmocones; holotype UTGD121138, paratypes UTGD81151, 121139, 121140, 121141, 121142, 121143, 121144, 121145 and 121146 all from the lower half of the Lower

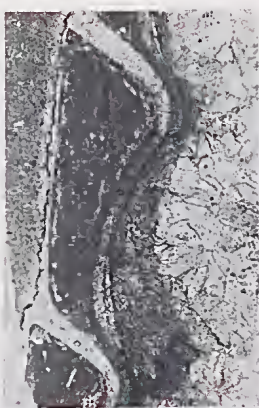
Fig. 10—A-J, *Gouldoceras benjaminense* sp. nov. A, sagittal section of the holotype, UTGD121129, venter left, $\times 4$. B, enlargement of the siphuncle at the adapical end of UTGD121129, venter left, $\times 10$. C, enlargement of the siphuncle at the adoral end of UTGD121129, venter left, $\times 10$. D, enlargement of the 'diaphragms' across the siphonal space, UTGD121129, venter left, $\times 24$. E, enlargement of the dorsal side of the siphuncle showing the radial spaces and the siphonal deposits, UTGD121129, $\times 20$. F, enlargement of the siphonal spaces at the apicad end of UTGD121129, venter left, $\times 24$. G, opaque section of the ventral side of the siphuncle showing the thick connecting ring, UTGD121129, venter left, $\times 20$. H, thin-section of UTGD121130, venter left, $\times 7$. I, enlargement of the 'diaphragm', UTGD121130, $\times 15$. J, enlargement of the siphonal spaces in UTGD121130, venter left, $\times 15$. K-N, Gouldoceratidae gen. nov. B. K, an external mould of the phragmocone wall showing two conchical furrows, UTGD22042, $\times 1$. L, sagittal section of UTGD22042, venter right, $\times 3$. M, enlargement of the dorsal wall of the siphuncle, UTGD22042, venter right, $\times 8$. N, enlargement of the ventral wall of the siphuncle, UTGD22042, venter right, $\times 8$.



A



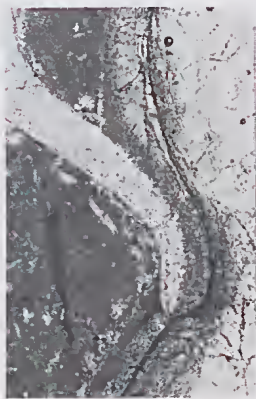
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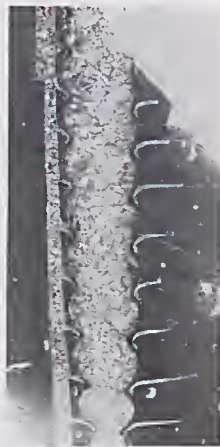
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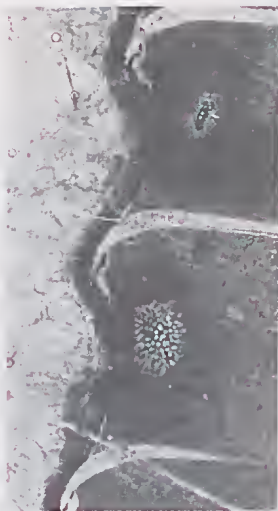
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K



L

Limestone Member of the Benjamin Limestone at Settlement Road section in the Florentine Valley (locality 4 on Fig. 4).

DERIVATION OF NAME. In honour of Dr. M. R. Banks contribution to Tasmanian palaeontology.

DESCRIPTION: The phragmocone is a subcircular, orthoconic longicone, with the venter slightly flattened. The phragmocone is slowly expanding, subtending an angle of 7° at the apex. The siphuncle is one-tenth of the diameter of the phragmocone. The siphuncle is approximately midway between the centre and the venter, but during growth moves relatively closer to the ventral phragmocone wall. In the holotype there are 35 siphuncular segments in a distance of 32 mm. The siphuncular segments are expanded, but prior to the shift towards the venter the segments are less expanded than after it. Prior to the ventral shift of the siphuncle the segments slope adorally from the venter to the dorsum but after the change the segments are normal to the siphuncular axis. The septa are only slightly curved, with the point of maximum depth at the siphuncle.

The siphonal formula of the holotype is 2.7/0.7/7.1:2.2/1.6/6.7;0.8 adorally, while apically it is 2.5/0.5/4.6:2.3/1.0/4.3;0.9.

The connecting rings are not adnate to the septa. They are thick and layered. There is a thick light layer on the cameral surface and a thin dark layer on the siphonal surface. Although the connecting rings have been partly recrystallized there is no indication that the rings contained any more complex differentiation. The septal necks and brims are short and cyrtchoanitic. The septal necks are not clearly preserved in the asymmetric portion of the phragmocone, but they appear to be short and cyrtchoanitic. Adorally on both the venter and the dorsum the septal necks are 0.2 mm long while the brims are 0.1 mm long. The siphonal deposits in the adapical asymmetric segments are parietal, forming in the septal foramina then growing apically along the connecting ring and over the deposit in the next segment to form endocones. The fine structure of the endocones is not preserved in any of the specimens found. In the adoral segments there are no deposits. Cameral deposits are present but have been largely recrystallized. Both hyposeptal and episepal deposits formed at the same time, and developed at about the same rate. The deposits are formed to a similar extent ventrally and dorsally. Cameral deposits are rarely present and appear to have formed only in the camerae which have the symmetrical siphuncular segments. This distribution may in-

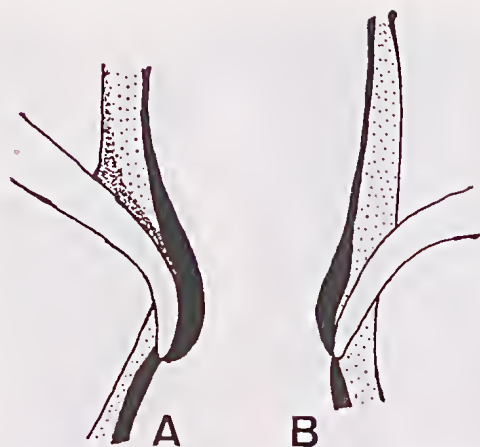


Fig. 12—The ventral (A) and dorsal (B) septal necks of *Benjaminoceras lauriei* UTGD121132, $\times 25$.

dicate that they formed late in growth, possibly after the asymmetric segments had been isolated by the diaphragms. The conch wall structures are preserved in this species and consist of three layers, firstly the inner layer which is formed by the mural part of the septum (0.005 mm thick), secondly a thick (0.2 mm) central lighter layer which appears to be structureless, and finally a thin (0.05 mm) darker layer on the outer surface.

REMARKS: See generic remarks.

Genus *Westfieldoceras* gen. nov.

TYPE SPECIES: *Westfieldoceras taylori* sp. nov.

DERIVATION OF NAME: The specimens were collected from the Westfield section in the Florentine Valley.

DIAGNOSIS: The phragmocone is a subcircular, orthoconic longicone, with the venter slightly flattened. The siphuncle is close to the venter but not in contact. The siphuncular segments are highly expanded. The siphuncular deposits consist of parietal deposits which first form in the septal foramen and then extend adapically along the connecting ring until they meet the adjacent deposit, forming a continuous lining. The septal necks are long and recurved, brims also long and recumbent to the septal necks. The connecting rings are thick and layered with a thin dark band on the siphonal surface and a thick lighter band on the cameral surface. The connecting rings are strongly adnate to the septa,

Fig. 11—*Benjaminoceras lauriei* gen. et sp. nov. A, sagittal thin section of the holotype, UTGD121132, venter left, $\times 2$. B, sagittal thin-section of UTGD121135, venter right, $\times 2$. C, ventral wall of the siphuncle, UTGD121132, 15. D, dorsal wall of the siphuncle, UTGD121132, venter left, $\times 10$. E, ventral septal neck, UTGD121132, $\times 25$. F, dorsal septal neck, note the fine structure of the unrecrystallized part of the siphonal deposits, UTGD121132, $\times 25$. G, sagittal section of UTGD121133, venter left, $\times 1$. H, ventral side of the siphuncle of UTGD121133, venter left, $\times 8$. I, dorsal wall of the siphuncle in UTGD121133, venter left, $\times 8$. J, thin-section of UTGD121134, venter right, $\times 1.5$. K, ventral phragmocone wall of UTGD121134, venter right, $\times 5$. L, enlargement of the connecting ring on the ventral side of the siphuncle in UTGD121134, venter right, $\times 8$.



Fig. 13—The ventral septal necks and connecting ring of *Benjaminceras laurie* UTGD121134, $\times 10$.

with the adoral part of the ring adnate for a short distance to the adapical face of the septum, while the adapical portion of the connecting ring is adnate for some distance to the adoral face of the septum. There are no cameral deposits.

REMARKS: *Westfieldoceras* is unusual as its morphology is reminiscent of two different orders. The septal necks and brims are very similar to those in *Lambeoceras* and it is assignable to the Huronidae of the Actinocerida. However, detailed examination of the connecting rings and siphuncular deposits show that *Westfieldoceras* is a discosorid assignable to the Gouldoceratidae and not an actinocerid. The most closely related genus is Gouldoceratidae gen. nov. C but this genus differs from *Westfieldoceras* in that its septal necks are not recurved, the siphuncle is in contact with the ventral wall of the phragmocone and the septal brims are short and free.

Westfieldoceras taylori sp. nov.

Figs 15F-K, 16

DERIVATION OF NAME: After Mr. M. Taylor who collected the first specimens.

MATERIAL: Three phragmocones, holotype UTGD95793, paratypes UTGD121158 and 121159 all from the Upper Limestone Member of the Benjamin

Limestone, at the Westfield section in the Florentine Valley (locality 3 on Fig. 3). The age is Eden.

DESCRIPTION: The phragmocone is a subcircular, orthoconic longicone, with the venter slightly flattened. The phragmocone is probably slowly expanding. The holotype consists of 28 segments in a length of 90 mm, the siphuncle is one-quarter of the height of the phragmocone. The siphuncular segments are expanded, and the middle of the segment is the point of maximum expansion. The siphuncle is between the centre and the venter, but is not in contact with the ventral wall. The septa are gently curved, with the point of maximum depth at the centre of the phragmocone.

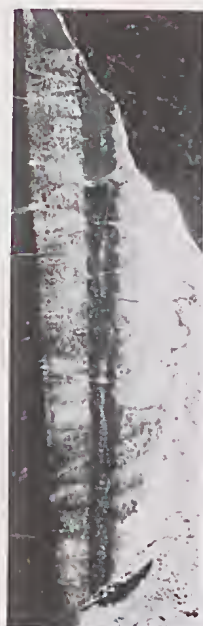
The siphonal formula is $2(+)/6/19(+); 1(+)/11/17(+); 4$ adorally, while apically it is $3.5(+)/5/29(+); 1(+)/10/26(+); 4$.

The connecting rings are strongly adnate to the septa on the venter, and less strongly adnate to the septa on the dorsum. On the venter the adapical portion of the connecting ring is adnate to the adoral side of the septum for a distance of 1.3 mm, while the adoral portion of the connecting ring is adnate to the adapical side of the septum for 2.0 mm. On the dorsum the corresponding measurements are 0.9 mm and 1.0 mm. The septal necks are long and recurved, the septal brims are also long and recumbent to the septal necks. Both the necks and brims have been recrystallized in the holotype and the paratype, UTGD121158, has only the venter preserved. The length of the necks and brims are variable from one segment to another, as is the degree of recurving. Ventrally the neck is 1.1 mm long, and the brim is 0.8 mm long, while on the dorsum the neck is 1.5 mm and the brim is 1.2 mm. The siphonal deposits are extensively developed in the adapical portion of the specimens. The deposits consist of parietal deposits which form in the septal foramen and then grow adapically along the connecting ring. The deposits are thickest in the middle of the segment and thinner at the septal foramen. The deposits have a thinly laminated structure parallel to the siphonal surface. The deposits grow until they meet the adoral end of the next most adapical deposit and thus form a continuous lining. The adapical segments are unknown so there is no indication of whether or not the deposits form closed endocones, but as this happens in all the other members of the Gouldoceratidae it is also probably true for *Westfieldoceras*. The connecting rings are thick and consist of two layers. The two layers are, a thin dark band on the siphonal surface and a thick lighter band on the cameral surface. On the paratype, UTGD121158, the

Fig. 14—*Paramadiganella banksi* gen. et sp. nov. A, opaque sagittal section of the holotype, UTGD121138, venter left, $\times 4$. B, opaque sagittal section of UTGD121141, venter left, $\times 3$. C, opaque section ground up from the venter of UTGD81151, $\times 2$. D, thin-section of UTGD121139, after the change in position of the siphuncle, venter left, $\times 10$. E, enlargement of the dorsal side of the siphuncle in UTGD121139, venter left, $\times 20$. F, sagittal thin section of UTGD121140, before the change in shape, venter right, $\times 20$. G, enlargement of an opaque section of the apical end of the holotype, venter left, $\times 14$. H, thin-section of UTGD121140 showing the connecting rings, venter left, $\times 20$. I, thin-section of the ventral septal neck in UTGD121139, venter left, $\times 30$. J, thin-section of the dorsal septal neck in UTGD121139, venter left, $\times 30$.



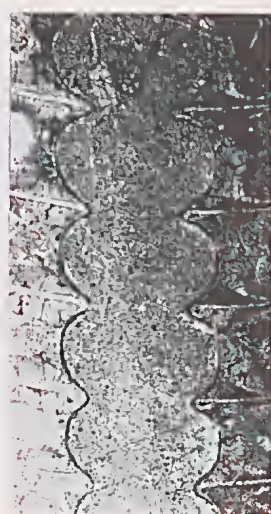
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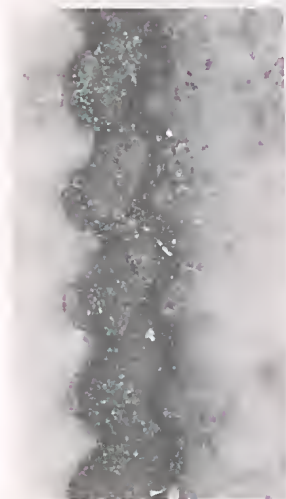
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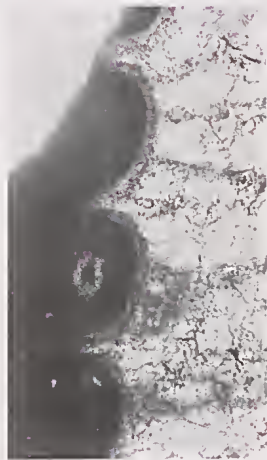
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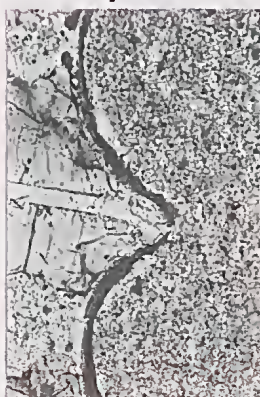
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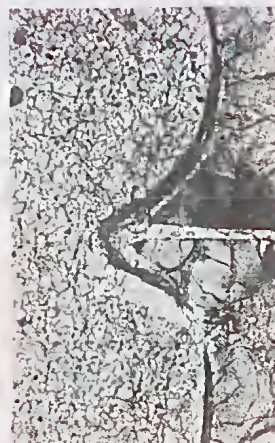
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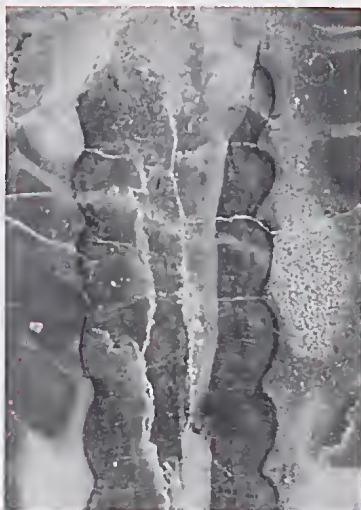
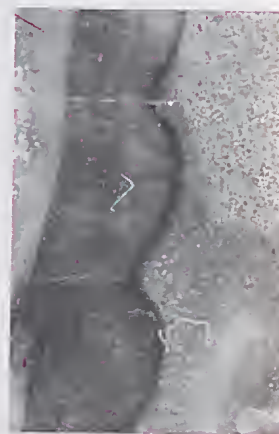
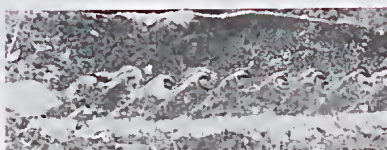
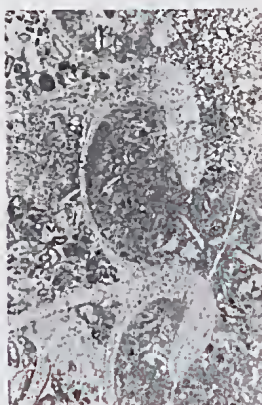
H



I



J

**A****B****C****D****E****F****G****H****I****JK**

lighter band appears to be made up of two layers, a dark inner band and a lighter band on the cameral surface, these two bands are of approximately equal thickness. There are no cameral deposits.

REMARKS: See generic remarks.

Genus *Tasmanoceras* Teichert & Glenister 1952

1952 *Tasmanoceras* Teichert & Glenister, p. 739.

1953 *Tasmanoceras* Teichert & Glenister; Teichert & Glenister, p. 16.

1964 *Tasmanoceras* Teichert & Glenister; Teichert, p. K179.

1968 *Tasmanoceras* Teichert & Glenister; Flower, p. 83.

TYPE SPECIES: *Tasmanoceras zeehanense* Teichert & Glenister 1952.

DIAGNOSIS: (emend. Stait herein from Teichert & Glenister 1952). Small discosorids with slowly expanding straight or weakly curved siphuncles. The siphuncle is half the diameter of the phragmocone. The siphuncle segments are slightly expanded between the septa, sloping at a moderately high angle to the axis of the siphuncle, adapically from the venter to the dorsum. The septal necks are slightly recurved cyrtchoanitic to hemichoanitic. The siphuncular deposits are finely laminated endocones which develop leaving only a siphonal space which varies in position from the centre to the dorsal side of the siphuncle. The central space may or may not be crossed by diaphragms. The connecting rings are thick and two-layered with a thin dark layer on the siphonal surface and a thick lighter layer on the cameral surface. No cameral deposits are known.

REMARKS: Teichert and Glenister (1952) established *Tasmanoceras* on two isolated siphuncles from Smelter's Quarry, Zeehan. Teichert and Glenister (1953) described another siphuncle of the type species from the Gordon River. They assigned *Tasmanoceras* to the endocerids mainly due to the presence of endocones. Flower (1968b, p. 83) noted the similarity between *Tasmanoceras* and *Donacoceras* and suggested that *Tasmanoceras* was a member of the Narthecoceratidae, which he included in the Michelinocerida. In the present study a great deal more material belonging to this genus has been collected and it is now clear that the similarities between *Tasmanoceras* and *Donacoceras* are homeomorphic. *Tasmanoceras* has thick connecting rings, with cyrtchoanitic to hemichoanitic septal necks and it has the fine laminated endocones typical of the



Fig. 16—The ventral septal necks and connecting ring of *Westfieldoceras taylori* UTGD121158, $\times 10$. Spaced stipple indicates the siphonal deposits, while the close stipple indicates the connecting ring.

Gouldoceratidae. *Tasmanoceras* differs from Gouldoceratidae gen. nov. A in having a siphuncle greater in diameter relative to the phragmocone, a siphuncle in contact with the ventral wall and in having less recurved septal necks. *Tasmanoceras* differs from *Benjaminoceras* in its shorter and more highly expanded segments and much longer and more recurved septal necks.

Tasmanoceras zeehanense Teichert & Glenister 1952 Fig. 17

1952 *Tasmanoceras zeehanense* Teichert & Glenister, p. 739, pl. 104, figs 3-9.

1953 *Tasmanoceras zeehanense* Teichert & Glenister; Teichert & Glenister, p. 16, pl. 4, figs 4, 5.

MATERIAL: Eight isolated siphuncles and one incomplete phragmocone. The specimens are UTGD121147, 121148, 121149, 121150, 121151, 121152, 121153, 121154 and 121155 from the Lower Limestone Member of the Benjamin Limestone in the Florentine Valley (localities 2, 6, 7 on Figs 3, 4).

DESCRIPTION: The phragmocone is straight, and the cross-section is subcircular, with the venter slightly flattened. The phragmocone is slowly expanding. In the

Fig. 15—A-E, Gouldoceratidae gen. nov. A., opaque sagittal section of UTGD121137, venter left, $\times 0.9$. B, enlargement of the siphuncle in UTGD121137, venter left, $\times 4$. C, opaque transverse section of the siphuncle in UTGD121137, venter below, $\times 8$. D, enlargement of the ventral wall of the siphuncle in UTGD121137, venter left, $\times 10$. E, enlargement of the dorsal wall of the siphuncle in UTGD121137, venter left, $\times 10$. F-K, *Westfieldoceras taylori* gen. et sp. nov. F, opaque sagittal section of the holotype, UTGD95793, venter left, $\times 1.5$. G, opaque sagittal section of UTGD121158, venter below, $\times 1$. H, opaque sagittal section of UTGD121159, venter right, $\times 2$. I, enlargement of the septal neck on the ventral side of UTGD121159, venter right, $\times 10$. J, thin-section of the dorsal septal necks and connecting rings in UTGD95793, venter right, $\times 8$. K, thin-section of the ventral septal necks and connecting rings of UTGD121158, venter left, $\times 10$.

holotype there are 15 siphuncular segments in 28 mm. The siphuncle is approximately half of the diameter of the phragmocone, and is in contact with the ventral wall, although the variability of the siphuncle means that in some segments they are not quite in contact with the wall. The septa are curved, with the point of maximum depth at the siphuncle.

The siphonal formula of UTGD121147 is $-/6.4/-/7.0/-/1.8$ apically while at the adoral end of the specimen it is $-/6.7/-/7.5/-/1.6$.

The adapical part of the connecting ring is adnate to the adoral surface of the septa for a short distance on both the ventral and dorsal sides of the siphuncle. The connecting rings are thick and composed of two layers. There is a thick, light layer on the cameral surface and a thinner dark layer on the siphonal surface. The septal necks are orthochoanitic and are on average 0.4 mm long. The length of the septal necks are variable both in an individual specimen and between different specimens. There is a continuum of lengths and this cannot be used as a species characteristic. The siphonal deposits consist of thin endocones which slope adorally at a low angle to the siphuncular axis. The endocones are wavy mimicking the outline of the siphuncular segments, asymmetric and more strongly developed on the ventral side of the siphuncle. The position of the siphonal space is variable from almost central to very close to the dorsal wall of the siphuncle. There are no cameral deposits.

REMARKS: This description of specimens from the Florentine Valley belonging to the type species has been included as they show features not visible on either the holotype or paratype material. These descriptions are intended to supplement those of Teichert and Glenister (1952).

Tasmanoceras cf. *T. zeehanense* Teichert & Glenister 1952

Fig. 18F-H

MATERIAL: Two isolated siphuncles, UTGD56471a, 56471b from just south of a quarry at Mayberry near Mole Creek, State Grid. Ref. sheet 8114, 454980 (Fig. 1).

DESCRIPTION: The specimens are only isolated siphuncles. There are 21 siphuncular segments in 46 mm, which are expanded and slope adapically from the venter to the dorsum at 80°. The siphuncular segments are 2.5 mm long, 6.3 mm high at the septal foramen and 7.0 mm at the expanded part of the segment. The septa are poorly preserved but probably the adapical part of the connecting ring is adnate to the adoral surface of the septum ventrally. The dorsal wall

of the siphuncle is not visible. The septal necks are orthochoanitic and 0.4 mm long. The siphuncular deposits are thin and slope adorally at a low angle to the siphuncular axis. The endocones are asymmetric being strongly concentrated on the venter. The siphonal space is midway between the centre and the dorsal wall of the siphuncle. The connecting rings are thick and contain two layers, a thick lighter layer on the cameral surface and a thinner dark layer on the siphonal surface.

REMARKS: These specimens differ from *Tasmanoceras zeehanense* in having siphuncular segments longer than is typical. The preservation is such that very few diagnostic features can be seen so a new species is not established.

Tasmanoceras pagei sp. nov.

Figs 18A-E, 19

DERIVATION OF NAME: For Mr. M. G. Page who studied the stratigraphy and palaeoecology of the Benjamin Limestone in the Florentine Valley.

MATERIAL: One specimen, UTGD121156, with the ventral wall of the phragmocone from 450 m above the base of the Lower Limestone Member in the Settlement Road section, Florentine Valley (locality 8 on Fig. 4). The age is Trenton.

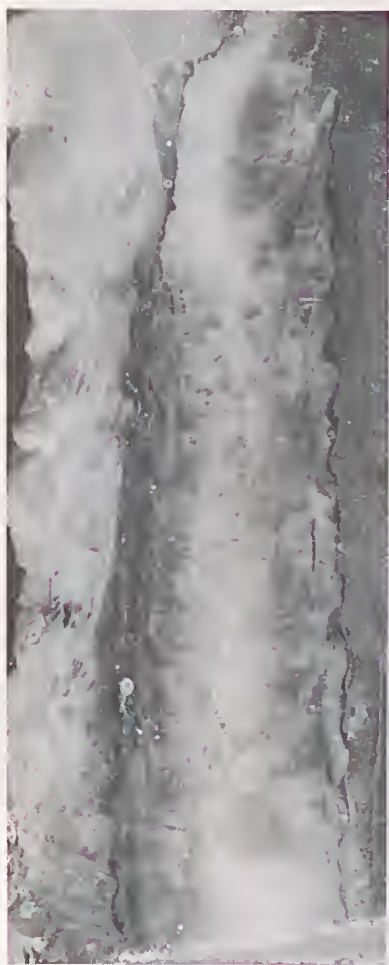
DESCRIPTION: Twenty-four siphuncular segments occur in a length of 28 mm. The siphuncle is close to the venter (however, the section is not quite sagittal and the siphuncle may be in contact with the ventral wall of the phragmocone). The siphuncular segments are expanded and slope apically from the venter to the dorsum at 70° to the axis of the siphuncle.

The siphonal formula is $1.0/4.7/-/0.7/6.5/-/1.2$ adapically while at the adoral end of the specimen it is $1.0/4.6/-/0.8/6.5/-/1.0$.

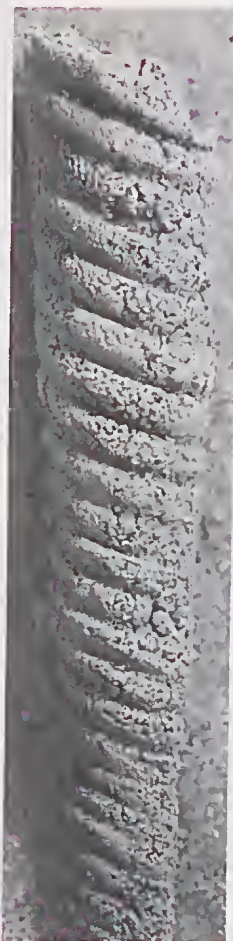
The connecting rings are not adnate to the septum dorsally, but ventrally the adapical part of the connecting ring is adnate to the adoral surface of the septum for a short distance. The septal necks are orthochoanitic and 0.4 mm long. The siphuncular deposits are composed of thin endocones, which slope adorally at a low angle to the siphuncular axis. The endocones are strongly asymmetric and are predominately developed on the venter. The endocones project much further forward on the venter than the dorsum. The siphonal space is near the dorsal wall of the siphuncle. The connecting rings are thick and composed of two layers. There is a thick, light layer on the cameral surface and a thinner dark layer on the siphonal surface.

REMARKS: The major difference between *T. zeehanense* and *T. pagei* is the ratio between the length and height

Fig. 17—*Tasmanoceras zeehanense* Teichert & Glenister 1952. A, opaque sagittal section of UTGD121147, venter right, $\times 3$. B, silicified isolated siphuncle UTGD121152, venter left, $\times 3$. C, transverse view of the endosiphococone of UTGD121152, venter below, $\times 5$. D, opaque sagittal section of the siphuncle of UTGD121148, venter left, $\times 3$. E, opaque sagittal section of UTGD121149, venter left, $\times 2$. F, opaque sagittal section of the ventral side of the siphuncle in UTGD121155, venter right, $\times 3$. G, enlargement of the septal necks and connecting rings in UTGD121150, venter right, $\times 30$. H, enlargement of the septal necks and connecting rings in UTGD81144, venter left, $\times 30$.



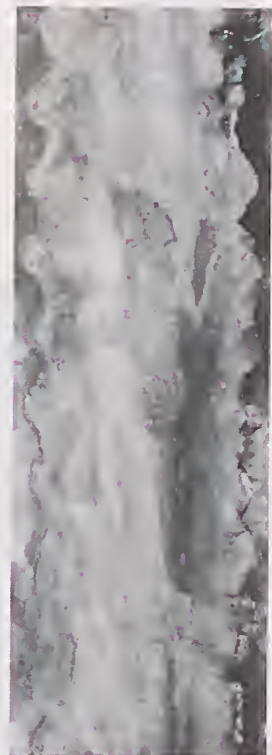
A



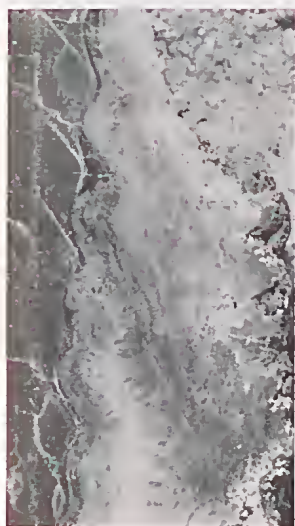
B



C



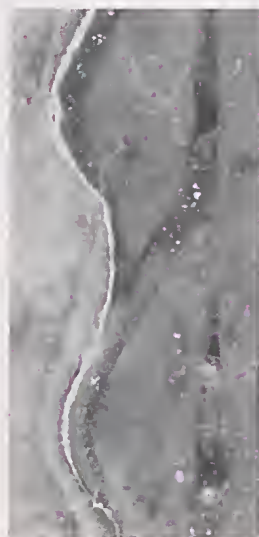
D



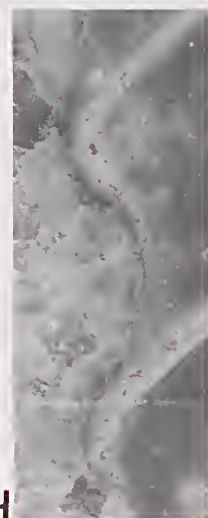
E

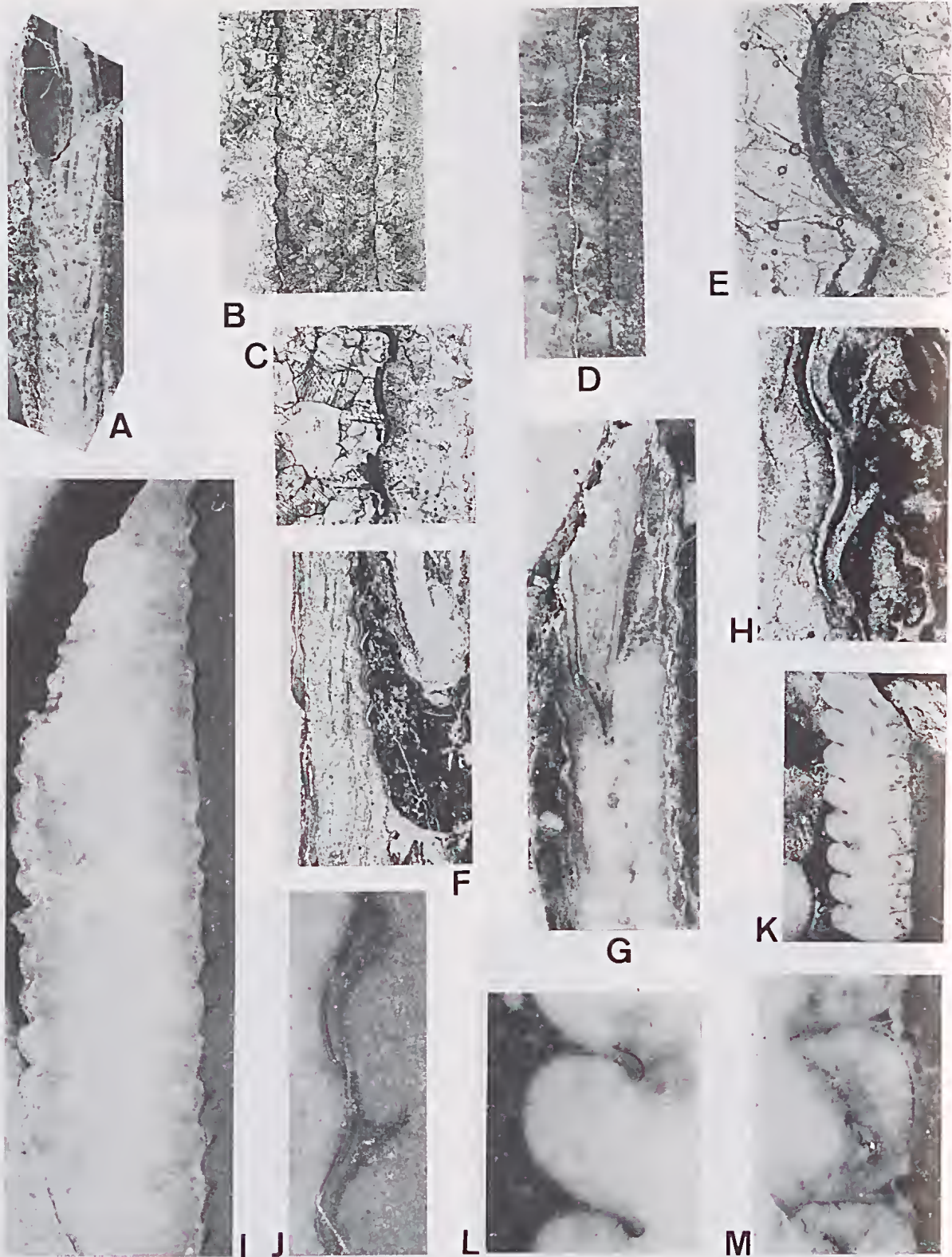


F



G H





of the siphuncular segments. *T. pagei* has much shorter segments relative to its height than does *T. zeehanense*. The only other consistent difference is that the curvature between the septal necks and the rest of the septa is almost a right angle in *T. pagei*, but in *T. zeehanense* it is gently curved and the septal necks are generally longer.

Tasmanoceras cf. *T. pagei* sp. nov.

Fig. 18I, J

REMARKS: UTGD121157 has been tentatively compared to *T. pagei* because of the very short siphuncular segments relative to their width. The specimen occurs stratigraphically below the holotype of *T. pagei* (locality 6 on Fig. 4), in association with *T. zeehanense*, it is not assigned to a species as the specimen is poorly preserved.

GOULDOCERATIDAE gen. nov. A, sp. nov.

Fig. 15A-E

MATERIAL: One partially preserved phragmocone, UTGD121137 from the Lower Limestone Member of the Benjamin Limestone at the Westfield section in the Florentine Valley (locality 1 on Fig. 3). The age is Chazy—Lower Blackriver.

DESCRIPTION: The phragmocone is a longiconic orthocone, subcircular in cross-section, venter is slightly flattened. There are 14 siphuncular segments in 39 mm. The phragmocone is probably slowly expanding. The siphuncular segments are moderately and evenly expanded. The siphuncle is one-fifth of the diameter of the phragmocone. The septa are gently curved with the point of maximum depth at the siphuncle.

The siphonal formula is 2.3/5.6/19:1.8/6.7/16.4; 2.5, while apically it is 2.1/5.3/17.8:1.8/6.4/17;2.5.

Recrystallization has made the septal necks difficult to recognise, but they are short and cyrtchoanitic, with the necks and brims similar in length. The necks are only preserved adorally where the necks are 0.3 mm long and the brim 0.1 mm long on the venter and the necks 0.2 mm long and the brims 0.1 mm long on the dorsum. The adapical portion of the connecting ring is adnate to the adoral face of the septum for a short distance, 0.3 mm on the venter and 0.4 mm on the dorsum. The connecting rings are thick and appear to have a thin dark layer on the siphonal surface and a thick layer on the cameral surface, although as only an opaque section



Fig. 19—The dorsal septal necks and connecting ring of *Tasmanoceras pagei* UTGD121156, $\times 25$.

is available detailed study of the connecting ring is difficult. The siphuncle contains well developed and extensive deposits. The deposits consist of finely laminated endocones composed of a light brown material with each of these layers separated by a very thin dark layer. The light layers are highly variable in thickness both from one layer to the next and also within each layer. The layers are wavy and mimic the outline of the siphuncular segments. There is also a radial structure which is normal to the connecting rings in longitudinal section and in transverse section radial from the siphonal space. The siphonal space is slightly to the dorsal side of the centre and contains diaphragms spaced at regular (approximately 5 mm) intervals along it. The endocones extend slightly further forward on the venter than the dorsum. There are no cameral deposits.

REMARKS: As this genus is represented by only one sagittally sectioned phragmocone it is left in open nomenclature. The expanded siphuncle, thin continuous endocones, and the thick two layered connecting rings indicate that this genus is a typical member of the Gouldoceratidae. The small size of the siphuncle relative to the phragmocone, the diaphragms and the relatively short siphuncular segments together distinguish this genus from other members of the Gouldoceratidae.

Fig. 18—A-E, *Tasmanoceras pagei* sp. nov. A, opaque sagittal section of the holotype, UTGD121156, venter right, $\times 1$. B, sagittal thin-section of the holotype, UTGD121156, venter right, $\times 2$. C, thin-section of the dorsal side of the siphuncle in UTGD121156, venter right, $\times 6$. D, opaque section of the ventral side of the siphuncle in UTGD121156, venter right, $\times 5$. E, enlargement of the septal neck and connecting ring on the dorsal side of UTGD121156, venter right, $\times 24$. F-H, *Tasmanoceras* cf. *T. zeehanense*. F, sagittal thin section of the isolated siphuncle of UTGD56471, venter right, $\times 4$. G, opaque sagittal section of UTGD56471, venter right, $\times 2.5$. H, enlargement of the ventral septal necks and connecting ring in UTGD56471, venter right, $\times 25$. I-J, *Tasmanoceras* cf. *T. pagei*. I, opaque sagittal section of the isolated siphuncle UTGD121157, venter right, $\times 4$. J, enlargement of the ventral wall of the siphuncle of UTGD121157, $\times 20$. K-M, Gouldoceratidae gen. nov. C., sp. nov., K, opaque sagittal section of the isolated siphuncle UTGD95796, venter right, $\times 1$. L, enlargement of the dorsal side of the siphuncle in UTGD95796, venter right, $\times 7$. M, enlargement of the ventral side of the siphuncle in UTGD95796, venter right, $\times 7$.

GOULDOCERATIDAE gen. nov. B, sp. nov.

Fig. 10K-N

MATERIAL: One partially preserved phragmocone, UTGD22042 from near the top of the Upper Limestone Member of the Benjamin Limestone, just below the track to Gordon Bend at the south end of the Tiger Range, State Grid. Ref. Wedge 8112; 499702, in the Florentine Valley.

DESCRIPTION: The dorsal phragmocone wall and camerae have been destroyed in the only specimen available. Based on the part of the phragmocone preserved it is probably an orthoconic longicone, with a rounded cross-section. The siphuncle is preserved only in the anterior part of the phragmocone and contains five segments in 18 mm, is probably relatively small, one-fifth or less of the diameter. The siphuncular segments are highly expanded, with the dorsal segments nearly symmetrical along their length, the ventral segments expand more rapidly in the adoral portion of the segment.

The siphonal formula is $2.4/6.3/-1.2/10/-;3.3$.

Ventrally the adapical part of the connecting ring is adnate to the adoral surface of the septum for a distance of 2.7 mm, the adoral portion of the ring is not adnate to the septum. Dorsally the adapical part of the connecting ring is adnate to the adoral surface of the septum for 1.8 mm, while the adoral part of the connecting ring is adnate to the adapical surface of the septum for 0.6 mm. The connecting rings are thick and layered with a thin dark layer on the siphonal surface and a thick lighter layer on the cameral surface. The connecting rings are 0.3 mm thick. The septal necks and brims are both short with the brims on the venter recumbent to the septum and on the dorsum very short and free. Ventrally the septal necks are 0.3 mm long, and the brims are 0.2 mm long, while dorsally the corresponding measurements are 0.6 mm and 0.2 mm. Recrystallization has obscured details of siphonal structures. The deposits are of the parietal type which form in the septal foramen and grow adapically through many segments to form endocones. The deposits are more extensively developed on the venter, with the siphonal space on the dorsal side of centre. There are no cameral deposits. The structure of the ventral wall of the phragmocone is preserved in this specimen. The shell wall is 1.2 mm thick. The shell consists of two major divisions, firstly the inner thick (1.1 mm) layer which is composed of many (12+) finer, alternating lighter and darker layers of variable thickness, and secondly an outer thin (0.1 mm) lighter layer. The outer layer is composed of many fine fibres which are normal to the layering in the inner layer.

REMARKS: The presence of thick two layered connecting rings and endocone like siphonal deposits indicate that Gouldoceratidae gen. nov. B is assignable to the Gouldoceratidae. It is most similar to *Westfieldoceras* in the size of the siphuncle relative to the phragmocone, but differs in that the siphuncle is in contact with the ventral wall of the phragmocone and the septal necks and brims are short and not as strongly recumbent.

Gouldoceratidae gen. nov. B is similar to the mature growth stage of *Benjaminoceras* in the type and form of the septal necks and brims, but differs from it in the shape and size of the siphuncle as *Benjaminoceras* probably has a relatively larger siphuncle.

GOULDOCERATIDAE gen. nov. C, sp. nov.

Fig. 18K-M

MATERIAL: Two isolated siphuncles UTGD95796 and 121160 from the upper part of the Upper Limestone Member of the Benjamin Limestone at the Westfield section in the Florentine Valley (locality 3 on Fig. 3).

DESCRIPTION: This species is only represented by isolated siphuncles. The siphuncle is in contact with the ventral phragmocone wall. There are eight siphuncular segments in 30 mm (UTGD95796). The siphuncular segments are highly expanded between the septal foramina and slope slightly adorally from the venter to the dorsum.

The siphonal formula at the fourth segment of UTGD95796 is $2/4/-0/9/-;3$.

The connecting rings are adnate to the septa both dorsally and ventrally. Ventrally the adoral part of the connecting ring is adnate to the adapical surface of the septa for a distance of 0.2 mm, while the adapical part of the connecting ring is adnate to the adoral surface of the septa for a distance of 1.0 mm. Dorsally the corresponding measurements are 1.0 mm and 1.0 mm. The connecting rings are thick. They have been largely recrystallized but there is an indication of a thin dark layer on the siphonal surface and a thick lighter layer on the cameral surface. The septal necks and brims are short and cyrochoanitic; the brims are recumbent on the septa. The necks and brims are of similar length both dorsally and ventrally, 0.1 mm long. The siphonal deposits have been completely recrystallized, although one specimen shows possible remnants of a siphonal space and radial spaces.

REMARKS: The preservation of these specimens makes assignment difficult. The presence of a thick two layered connecting ring suggests they are assignable to the Gouldoceratidae. The siphonal and radial spaces are similar to those in *Gouldoceras* itself. The siphuncles are unlike those of any other member of the Gouldoceratidae. They are most closely related to Gouldoceratidae gen. nov. B but the septal necks and the shape of the siphuncular segments are different from those in Gouldoceratidae gen. nov. B.

ACKNOWLEDGEMENTS

The author wishes to thank the following people, Dr M. R. Banks, Dr. C. F. Burrett, Dr. J. R. Laurie, Kathi Kenna, Clive Calver and Mike Page for their help during all stages of this project. For advice and valuable discussion Prof. C. Teichert, Dr. R. H. Flower, Dr. M. Wade and Prof. W. C. Sweet are gratefully acknowledged. Prof. C. Barnes allowed time for the completion of this work while the author was employed at Memorial University of Newfoundland. The following are thanked

for financial support, Australian Post Graduate Research Award Scheme, Australian Research Grants Scheme and the University of Tasmania, especially the special grants scheme.

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NEANTHES (POLYCHAETA: NEREIDIDAE) FROM VICTORIA WITH DESCRIPTIONS OF TWO NEW SPECIES

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ABSTRACT: Two nereidid polychaetes are described from Victoria, *Neanthes bassi* sp. nov. and *N. flindersi* sp. nov. *Neanthes succinea* Leuekart is recorded from Australia for the first time and the status of *Nectoneanthes* Imajima is discussed. A systematic account of *Neanthes* known from Victoria and a key to species recorded from southern Australia are provided. A list is appended of all species of *Neanthes* described to date.

During the years 1979-1983 the Museum of Victoria (previously National Museum of Victoria) made extensive collections of soft bottom benthos as part of a survey of the marine fauna of Bass Strait. This paper reports on nereidid polychaetes of the genus *Neanthes* collected during that survey and on additional material from other collections deposited in the Museum of Victoria.

MATERIALS AND METHODS

Locality data for all stations occupied during the Bass Strait Survey (BSS prefixes) are being published elsewhere (Wilson & Poore in press) and complete localities are only given here for type specimens. Sources for other collections included in this study are: the Port Phillip Bay Environmental Study (PPBES) (Poore *et al.* 1975, Poore & Kudenov 1978); littoral and benthic surveys of Western Port (Smith *et al.* 1975); Crib Point Benthic Survey (CPBS) and Westernport Bay Environmental Study (WBES) (Ministry for Conservation 1975, Coleman *et al.* 1978); Gippsland Region Environmental Study (GRES) (Poore 1982); N.S.W. Shelf Benthic Survey (SBS) (Jones 1977).

Registration numbers of Museum of Victoria material are prefixed NMV. Paratypes have been deposited at the Australian Museum, Sydney (AMW or AME, Endeavour material), British Museum (Natural History), London (BMNH) and the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM). Zoologisches Institut and Zoologisches Museum der Universität Hamburg is abbreviated to HZM and Western Australian Museum (Perth) is abbreviated to WAM.

The Australian distribution of each species is taken from Hutchings and Turvey (1982) and full Australian synonymies can be found in Day and Hutchings (1979). A key is provided to all species of *Neanthes* known from Victoria, Tasmania, South Australia and Western Australia south of Perth (32°S). All species have been recorded from Victoria and Bass Strait with the exception of *Neanthes isolata* Hutchings & Turvey 1982 which is known only from South Australia (Hutchings & Turvey 1982) and is not treated in the systematic text.

Diagnosis of species of *Neanthes* rely heavily on the number and arrangement of paragnaths on the pharynx, particularly on the oral ring and on the relative propor-

tions of the parapodial lobes, particularly on posterior setigers. In this study the distribution along the body of two types of neuropodial setae, heterogomph spinigers and heterogomph falcigers was found to provide useful additional characters with which to distinguish species. This information is presented for new and previously described species and is also used in the key to species. Identifying patterns in setal distribution requires location of the exact position at which a change occurs (e.g. the setiger at which heterogomph falcigers first occur). Preliminary investigations indicate that differences between left and right of the same setiger are not significant and where possible right side parapodia were examined for this study. Body width measurements given refer to width excluding parapodia.

KEY TO SPECIES OF NEANTHES FROM SOUTHERN AUSTRALIA

1. Notopodia with three approximately equal lobes throughout (median lobes may be reduced on posterior setigers of small specimens) 2
Notopodia with two lobes (small presetal lobe may be present anteriorly, usually setigers 10-20) 3
2. Oral ring paragnaths (Areas V-VIII) a continuous band 2-5 deep; Area I with more than 10 cones
..... *Neanthes cricognatha*
Oral ring paragnaths a centrally isolated group of up to 12 on VI, a broad band tapering to 1 row laterally on VII-VIII; Area I with fewer than 10 cones
..... *Neanthes succinea*
3. Area VI without paragnaths or with an isolated central group of paragnaths 4
Area VI with a transverse row of paragnaths 8
4. Area V with 0-1 paragnaths, VII-VIII with fewer than 30; neuropodia of at least first 10 setigers of specimens wider than 1 mm with digitiform postsetal process 6
Area V with 2-6 paragnaths (rarely 1), VII-VIII with more than 35; anterior neuropodia without prominent digitiform postsetal process 5
5. Area III with about 20 paragnaths or more, V with 3 in a triangle (rarely 1 or 2 but never in longitudinal series); specimens wider than 1 mm with presetal lobe in anterior notopodia, usually first 6-20 setigers (lives intertidally on sheltered coasts) *Neanthes vaalii*

- Area III with 8-16 paragnaths, V with 3-6 including 2-3 in longitudinal series; presetal notopodial lobe absent on all specimens up to at least 2 mm width (lives intertidally on exposed coasts) *Neanthes isolata*.
6. Area IV with smooth bars and conical paragnaths arranged in two triangles of approximately equal area; notopodia without presetal lobe; heterogomph falcigers first present in neuropodia at setigers 3-6 (rarely 2) *Neanthes bassi* sp. nov.
Area IV with conical paragnaths dominant, 1-3 smooth bars may be present also; specimens larger than about 1.5 mm body width with notopodial presetal lobe on a variable number of anterior setigers; heterogomph neuropodial falcigers present throughout, commencing setiger I 7
7. Area VI with 0-1, VII-VIII with 0-6 paragnaths
..... *Neanthes kerguelensis*
Area VI with 1-3, VII-VIII with 16-30 paragnaths *Neanthes flindersi* sp. nov.
8. Area VI with a single transverse row of larger paragnaths and occasional smaller ones, VII-VIII with mainly large cones, usually fewer than 50 *Neanthes uniseriata*
Area VI with 2 rows of large cones and a variable row of smaller cones, VII-VIII with large and small cones, usually more than 50 *Neanthes biseriata*

SYSTEMATICS

Genus *Neanthes* Kinberg 1866

DIAGNOSIS: Eversible pharynx with conical paragnaths on both rings. Four pairs of tentacular cirri, parapodia biramous. Notoetae homogomph spinigers; neuroetae homogomph and heterogomph spinigers and heterogomph falcigers (after Fauchald 1977a).

TYPE SPECIES: *N. vaalii* Kinberg 1866

SPECIES INCLUDED: See Appendix.

Neanthes bassi sp. nov.

Fig. 1

1971 *Platynereis australis* Schmarda; Knox & Cameron, p. 28. (partim)

MATERIAL: Holotype, NMVF50005 Bass Strait, N of Robbins Island, NW Tasmania (40°31'S, 144°56'E), 27 m very coarse shell, epibenthic sled, P. Forsyth *et al.* on F. V. Sarda, 2 Nov. 1980 (Stn BSS 109). Paratypes, NMVF50006-9, AMW198701-2, BMNHZB 1984. 47-48, USNM097289, 097280 all from type locality; Bass Strait, N of Robbins Island NW Tasmania (40°31'S, 145°04'E) 29 m, sand (Stn BSS 111 SEB), NMVF50010; Bass Strait, NE of Robbins Island, NW Tasmania (40°22'S, 145°17'E 40 m, sand (Stn BSS 112 SEB), NMVF50011. Additional Material, Bass Strait, E of Corner Inlet, (Stn BSS 178 TAM), NMVF50012-F50016; Bass Strait, S of Orbest, (Stn BSS 207 SEB), NMVF50017; Port Phillip Bay Survey Area 9 Stn 178, NMVF50123 (2 specimens); Port Phillip Bay Survey Area 55 Stn 148, NMVG1866 (part of material identified as *Platynereis australis* Schmarda 1861 by Knox & Cameron 1971).

Unpublished notes from the Port Phillip Bay Environmental Study (1969-1973) indicate that *Neanthes* sp. 1, species no. 471, PPBES Stn 984, 1 specimen and nereid sp. 2, species no. 690, PPBES Stn 928, 2 specimens (Poore *et al.* 1975, p. 50) may represent additional record(s) of *Neanthes bassi* sp. nov. However these specimens appear to have been lost.

DESCRIPTION: Holotype an anterior fragment of 36 setigers, 8 mm length, 1.5 mm maximum width. Colour in alcohol pale brown with darker brown pigmentation on prostomium and darker brown transverse bands on dorsum of apodous segment and first setiger. Prostomial length slightly exceeds width. Two pairs of eyes, pigmentation lost. One pair of stout palps with small globular palpostyles, one pair of antennae approximately equal in length to prostomium. Four pairs of tentacular cirri, faintly annulated, longest extending to setiger 4. Jaws large, translucent brown with 6 teeth. Pharynx with conical paragnaths on both rings and smooth bars also present on Area IV only, arranged as follows: I=1; II=13, 15 in two crescent shaped rows; III=6 in a single transverse row; IV=a triangle of 7 cones and also a triangle of 5 smooth bars; V=1; VI=8, 6 in a roughly circular patch; VII-VIII=9 in a single row.

Notopodia with two approximately equal lobes, presetal notopodial lobe absent, dorsal cirrus of approximately equal length to notopodial lobes, becoming approximately 1.3 times longer on posterior setigers. Notopodia becoming elongate, approximately 1.5 times longer than neuropodia on posterior setigers. Neuropodia bilobed, lobes approximately equal on anterior setigers, ventral lobe becoming reduced posteriorly, neuropodial digitiform postsetal process present on setigers 1-6. Ventral cirrus basally attached, approximately half length of neuropodium throughout (Fig. 1b, c). Notoetae homogomph spinigers from setiger 3 (setigers 1 and 2 uniramous). Dorsal fascicle of neuroetae include homogomph and heterogomph spinigers on setigers 1-5, joined by heterogomph falcigers (Fig. 1d, e) from setiger 7. Ventral fascicle of neuroetae include heterogomph spinigers only, on anterior setigers, plus heterogomph falcigers from setiger 7.

VARIATION: Variations not described for the holotype based on 11 paratypes (anterior fragments, size range 14 setigers, 3 mm length, less than 1 mm width, to 35 setigers, 17 mm length, 3 mm width) and on additional material listed above (largest specimen entire, 106 setigers, 51 mm length, 3 mm width, NMVG1688). Dorsum of a variable number of anterior setigers often with a pair of dark brown patches. Antennae equal to or slightly exceeding length of prostomium. Tentacular cirri faintly annulated, longest extending to setiger 4-9. Pharynx with conical paragnaths on both rings and smooth bars also present on Area IV only, arranged as follows: I=0-1 (rarely 2 or 3 in longitudinal series); II=6-27 in two crescent shaped rows; III=1-13; IV=a triangle of 3-18 cones and also a triangle of 3-7 smooth bars (Fig. 1a); V=0-1; VI=2-9 in a roughly circular patch; VII-VIII=5-29 in 1-2 rows decreasing laterally.

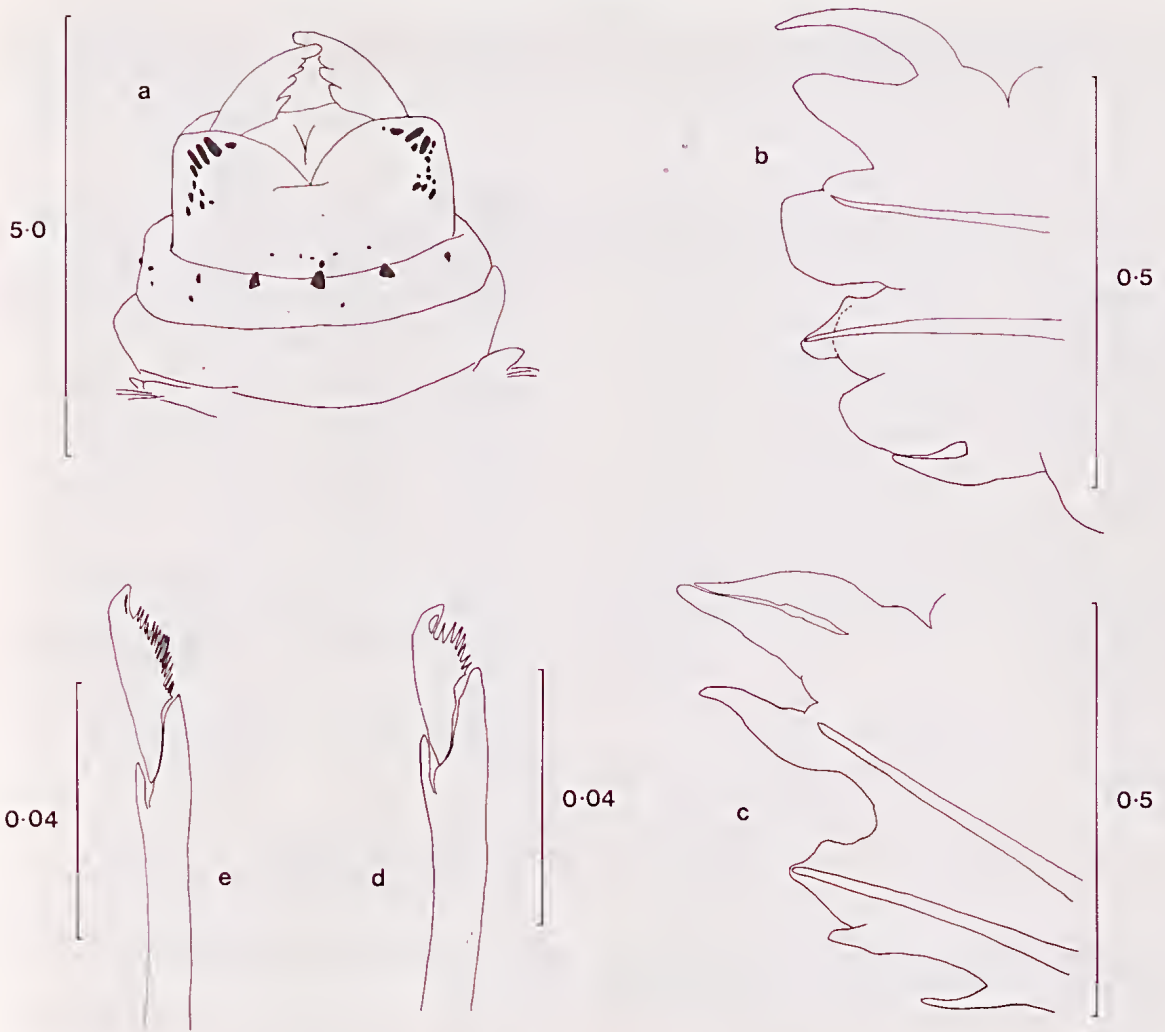


Fig. 1—*Neanthes bassi* sp. nov. a, ventral view of everted pharynx (paratype NMVF50006). b, anterior view of 10th parapodium (holotype NMVF50005). c, anterior view of 32nd parapodium (holotype NMVF50005). d, ventral neuropodial heterogomph falciger, setiger 10 (holotype NMVF50005). e, ventral neuropodial heterogomph falciger, setiger 32 (holotype NMVF50005). Scales in mm.

Specimens exceeding about 1 mm body width with neuropodial digitiform postsetal process on anterior 5-10 setigers. Heterogomph falcigers appear in dorsal neuropodial fascicle from setigers 4-6 and in ventral neuropodial fascicle from setigers 4-7. One specimen, NMVF50014, has heterogomph falcigers present in the neuropodium at setiger 2. However in all other respects this specimen agrees with the description given here. Heterogomph spinigers are present in both neuropodial fascicles from setiger 1 but are replaced posteriorly by homogomph spinigers. Homogomph spinigers do not appear before setiger 7-8 and heterogomph spinigers persist as 1-2 setae in the dorsal region of the ventral neuropodial fascicle back to setigers 12-40.

Anal cirri extend back 17-25 setigers on the only two specimens which are complete posteriorly (NMVG1688).

No specimen examined has obvious coelomic gametes.

REMARKS: Fauchald (1972) subdivided *Neanthes* on the presence or absence of falcigers and on the relative development of parapodial lobes. *Neanthes bassi* belongs to his Group IIB 1 with notopodial lobes approximately equal in size and of similar relative proportions posteriorly. Within this group 12 species are similar to *N. bassi* in that paragnath counts include a group of fewer than 20 on Area III, a roughly circular group on VI and a band of 1-2 rows on VII-VIII. *Neanthes* (*Hediste*) *diversicolor* (Müller 1776), *N. limnicola* (Johnson 1903), *N. japonica* Izuka 1908 and *N. unifasciata* (Wiley 1905) are all estuarine forms and can be distinguished from *N. bassi* by their fused simple falcigers in the posterior neuropodia. The remaining 8

TABLE 1

Neanthes GROUP IIB 1 (PART; EMENDED AFTER FAUCHALD 1972). COMPARISON OF SPECIES LACKING FUSED FALCIGERS, WITH FEWER THAN 20 PARAGNATHS ON AREA III, WITH A CIRCULAR GROUP ON AREA VI AND A BAND OF 1-3 ROWS ON AREAS VII-VIII.

	Area I	Area III	Area V	Area VI	Area VII-VIII	Presetal (3rd) notopodial lobe (anterior)	Postsetal (3rd) neuropodial lobe (setigers)	Source of data
<i>N. bassi</i> sp. nov.	0-3 (LS)	1-13	0-1	2-9	5-29 (1-2 R)	absent	present	this study
<i>N. flava</i> Wu Baoling & Sun Ruiping 1981	1	1	0	6-7	40-60	present	absent	Wu Baoling & Sun Ruiping 1981
<i>N. galetae</i> Fauchald 1977b	2	18	0	8	5 (1 R)	absent	present	Fauchald 1977b
<i>N. indica brunnea</i> Day 1957	2-3 (LS)	7-10	0	6	2-3 R	present	present	Day 1957
<i>N. isolata</i> Hutchings & Turvey 1982	1-2 (LS)	8-12	3-6	6-11	37-55 (2-3 R)	present	absent	Hutchings & Turvey 1982
<i>N. macrocephala</i> Hansen 1882	2 (LS)	13	2 (1 R)	7	2-3 R	not recorded	not recorded	Hansen 1882
<i>N. nanhaiensis</i> Wu Baoling & Sun Ruiping 1981	0-1	1-5	0	0-2	1-4 (1 R)	present	present	Wu Baoling & Sun Ruiping 1981
<i>N. vaalii</i> Kinberg 1866	1-4 (LS)	19-28	1-3	3-5	37-59 (2-3 R)	present	absent	this study
<i>N. virens</i> (Sars 1835)	0-7	4-14 (2-3 R)	0-4	0-5	2-3 R	present	present	Pettibone 1963

Explanation of abbreviations: × R = × transverse rows of paragnaths; LS = in longitudinal series.

species can be distinguished from *N. bassi* using the characteristics given in Table 1. In this study, *N. virens* (Sars 1835), has been moved from Group I to Group IIB 1. See Remarks under *N. succinea*, below.

Among the species of *Neanthes* known to occur in southern Australia, *N. bassi* most closely resembles *N. vaalii* Kinberg 1866. However, the two species differ not only as shown in Table 1 but also in the distribution of neurosetae: *N. bassi* lacks heterogomph falcigers on a variable number of anterior setigers and lacks heterogomph spinigers on a variable number of posterior setigers in contrast with *N. vaalii* in which both heterogomph spinigers and falcigers are present in all neuropodia.

Neanthes bassi also appears to differ from all species presently described for the genus in the degree of development of bar shaped paragnaths on Area IV. The presence of paragnaths with transversely elongated bases along with cones was noted on Area IV of *N. nanciae* (Day 1949, p. 445) and in the course of the present study bar paragnaths were noted on Area IV of *N. isolata* Hutchings & Turvey 1982, *N. vaalii*, *N. biseriata* Hutchings & Turvey 1982, and *N. uniseriata* Hutchings & Turvey 1982. In each case bars are situated close to the base of the maxillae but in no other species are they developed to the extent that they equal or exceed the

area occupied by cones on Area IV as in *N. bassi* (Fig. 1a).

ETYMOLOGY: *Neanthes bassi* is named after George Bass, who first navigated Bass Strait.

DISTRIBUTION: Southwestern and northeastern Bass Strait and Port Phillip Bay, Victoria. Known only from southeastern Australia.

HABITAT: Various sand shell and mud sediments, 7-51 m.

Neanthes cf. *N. bassi* sp. nov.

MATERIAL EXAMINED: Stn BSS 170 GSM, NMVF50018; Stn BSS 170 SEB, NMVF50019-F50021.

REMARKS: Four specimens from Stn BSS 170 in eastern Bass Strait appear to be closely allied to *N. bassi* but their identification must remain doubtful until more material is available. These specimens differ from *N. bassi* as shown in Table 2.

Neanthes biseriata Hutchings & Turvey 1982

1982 *Neanthes biseriata* Hutchings & Turvey, p. 108, fig. 6a-e, table 6.

MATERIAL EXAMINED: W.A.-Emu Point, Albany, coll. 6 Jan. 1973, WAM79-74 (includes 1 immature female epitoke).

S.A.—Speeds Point, Streaky Bay (04A), 4 paratypes, AMW18423; Venus Bay (06B), 40 paratypes, AMW18418; Victor Harbour (18A), 46 paratypes, AMW18420; Encounter Bay coll. 3 Jan. 1977, AMW194928 (full locality data given by Hutchings & Turvey 1982).

Tas.—Goose Island, coll. 20 Jan. 1979, NMVF50130.

Vic.—Kilcunda, coll. Jan. 1966, NMVF50061, F50063, F50065; Somers, Western Port, NMVF50062 (2 specimens); Point Leo, Western Port, F50064 (4 specimens); Flinders, Western Port, coll. 30 Jan. 1967, NMVF50066 (4 specimens); Flinders, Western Port, coll. 13 Jan. 1968, NMVF50067 (2 specimens); Sunderland Bay, Phillip Island, coll. 9 Dec. 1977, NMVF50068 (40 specimens); Kitty Miller Bay, Phillip Island, NMVF50069 (8 specimens); East of Grey River, Otways Coast, coll. 14 Aug. 1983, NMVF50070 (3 specimens); Corner Inlet, Doughboy Island, coll. 24 Nov. 1983, NMVF50160 (6 specimens).

DESCRIPTION: Size range of material examined 52 setigers, 9 mm long, <1 mm wide to 60 setigers, 26 mm long, 2 mm wide (entire specimens). Pharynx with conical paragnaths on all Areas, some specimens with a few short bars also present on Area IV, arranged as follows (counts based on 36 specimens including II from the type series): I=2-8, usually 5-6; II=8-22; III=20-34; IV=18-33 cones and 0-3 short bars; V=9-19; VI=3-12, usually 7-10 in 2 rows; VII-VIII=66-115 large and small cones.

Notosetae all homogomph spinigers. Neurosetae heterogomph falcigers and homogomph spinigers in the dorsal fascicle and heterogomph falcigers and heterogomph spinigers in the ventral fascicle.

REMARKS: The description given here differs slightly from the original description of Hutchings and Turvey

(1982). They reported paragnath counts of V=3-7 and VI=11-24 whereas the material examined in this study is in the range V=9-19 and VI=3-12 (usually 7-10). The material examined here represents a wider size range than was available to Hutchings and Turvey. However, the differences also result in part from differing interpretations of the borders of Area VI: in the present study, counts for Area VI include only those paragnaths which make up the double row which is characteristic of *N. biseriata*.

Hutchings and Turvey reported homogomph spinigers in the ventral neuropodial fascicle in *N. biseriata*. The material examined in this study and Hutchings' and Turvey's working notes (Hutchings pers. comm.) confirm that the only setal types present in the ventral neuropodial fascicle are heterogomph spinigers and heterogomph falcigers.

Except as noted above the material examined here conforms to the description of Hutchings and Turvey (1982). The range of *N. biseriata* is here extended to include Western Australia, Victoria and Tasmania.

DISTRIBUTION: Western Australia, South Australia, Victoria and Tasmania. Known only from southern Australia.

HABITAT: Intertidal in algae and in rocks and sand.

Neanthes cricognatha Ehlers 1904

1904 *Neanthes cricognatha* Ehlers, p. 29, pl. 4, figs 3-7.

1982 *Neanthes cricognatha* Ehlers; Hutchings & Turvey, p. 110.

1971 *Neanthes caudata* delle Chiaje; Knox & Cameron, p. 28.

1975 *Neanthes* sp. 2 (sp. no. 604) Poore *et al.* p. 50.

MATERIAL EXAMINED: W.A.—Fremantle, NMVF50172. Bass Strait—Stn BSS 51 GSM, NMVF50166 (5

TABLE 2
COMPARISON OF *Neanthes bassi* sp. nov. AND *Neanthes* cf. *bassi* sp. nov.

	<i>N. cf. bassi</i> sp. nov. (n=4)	<i>N. bassi</i> sp. nov. (n=19)
Size range of material examined	14 setigers, 3 mm length, less than 1 mm width (anterior fragment) to 43 setigers, 9 mm length, 1.5 mm width (entire specimen)	14 setigers, 3 mm length, less than 1 mm width (anterior fragment) to 106 setigers, 51 mm length, 3 mm width (entire specimen)
Paragnaths on I	2-4	Usually 0-1 (3 on one specimen 3 mm wide)
Paragnaths on IV	2 specimens only have faint bars on one side	3-5 bars always present on both sides
Paragnaths on VII-VIII	5-8	10-20
Notopodia	Presetal lobe present in all specimens exceeding 1.5 mm width	Presetal lobe absent in specimens of all sizes
Neuropodia	Digitiform postsetal process present setigers 1-18 (1-11 on specimens less than 1 mm width)	Digitiform postsetal process present setigers 1-10 (absent on specimens less than 1 mm width)
Heterogomph falcigers appear in neuropodia	Setiger 2-3	Setiger 5-6 (rarely 2)
Pairs of dark patches on anterior dorsum	Absent	Usually present
Habitat	Mud sediment, 130-140 m	Variety of sediments, 18-51 m

specimens); Stn BSS 83 DP, NMVF50167; Stn BSS 138 trawl, NMVF50168 (2 specimens); Stn BSS 155 SEB, NMVF50169 (3 specimens); Stn BSS 194 SEB, NMVF50170; Stn BSS 201 SEB, NMVF50171 (5 specimens). Additional material, NMV unregistered: Stns BSS 58, 59, 77, 81, 107, 108, 111, 112, 117, 127, 128, 134, 137, 153, 155, 158, 162, 170, 173, 178, 188, 197, 200, 203, 205, 207, 209 (total of 51 specimens).

Victoria—Werribee, Port Phillip Bay, coll. Aug. 1977, NMVF50079; Port Phillip Bay (Area 59 Stn 36, Knox and Cameron, 1971), NMVG1631; Port Phillip Bay, PPBES Stns: 907, 945, 974, NMV 3 unregistered specimens; West of Eagles Nest, coll. 19 Feb. 1966, NMVF50082; Shoreham, Western Port, coll. 20 Dec. 1965, NMVF50080; Flinders, Western Port coll. 31.1.1967, NMVF50081 (14 specimens); Western Port CPBS: Stn 21N, NMVF50164-5; Stn 32N, NMVF50161-2 (3 specimens); Stn 51N, NMVF50163; Corner Inlet, 4 km SE Barry Beach, coll. 24 Nov. 1983, NMVF50173 (2 specimens); Corner Inlet, 0.5 km S Granite Island, coll. 23 Nov. 1983, NMVF50174. Additional material, NMV unregistered, Western Port CPBS Stns 31S, 31N, 32S, 32N (total of 20 specimens).

N.S.W.—SBS: North Head, Sydney, 29 m, AMW198371 (2 specimens); Stn A2 sample 4, AMW198375; Stn B3 sample AMW198372; Stn C1 sample 5, AMW198374 (10 specimens); Stn D1 sample 2, AMW198373.

DESCRIPTION: Size range of material examined 25 setigers, 7 mm long, <1 mm wide to 32 setigers, 34 mm long, 4 mm wide (anterior fragments). Pharynx with conical paragnaths on all Areas arranged as follows (counts based on 23 specimens from Victoria and Bass Strait): I=9-16; II=22-45; III=23-45; IV=29-54; V-VIII a continuous band 3-5 deep dorsally, 5-8 deep ventrally. The largest paragnaths on the maxillary ring are found on Area II ('canine-like' curved teeth) and on the oral ring the largest paragnaths are those in the dorsal and dorsolateral positions (Areas V and VI).

Notopodia with three triangular lobes, neuropodia with two lobes and postsetal triangular process decreasing posteriorly. Notosetae homogomph spinigers, neurosetae homogomph spinigers and heterogomph falcigers throughout in dorsal and ventral fascicles. Heterogomph falcigers with long, almost rectangular blades and hooked distal tooth (figured by Ehlers 1904, pl. 4, fig. 5).

REMARKS: *Neanthes cricognatha* Ehlers 1904 has been synonymised with *N. caudata* (delle Chiaje 1828) and with *N. arenaceodentata* (Moore 1903) by Pettibone (1963), Day (1967), Imajima (1972) and Hartmann-Schröder (1982). I follow Hartman (1954) and Hutchings and Turvey (1982) in using the name *N. cricognatha* for Australian specimens. The Australian material examined in this study differs from material identified as *Nereis* (*Neanthes*) *caudata* from South Africa (Day 1967, p. 322, fig. 14.9i) in that the dorsal cirri of posterior setigers are located closer to the base of the notopodium than Day figured. The present material also differs from material encompassing a similar size range

identified as *N. caudata* from Japan (Imajima 1972) in that Area 1 has fewer paragnaths (9-16) than that reported by Imajima (I=16-18).

DISTRIBUTION: Western Australia, South Australia, Tasmania, Victoria, New South Wales. Also recorded from New Zealand.

HABITAT: Intertidal to 140 m deep, more common subtidally, mostly from soft bottoms.

Neanthes flindersi sp. nov.

Fig. 2

MATERIAL: Holotype, NMVF50022 Bass Strait, S of Cape Otway (39°06.0'S 143°35.8'E) 95 m, fine sand, epibenthic sled, M. Gomon *et al.* on RV Hai Kung, 31 Jan. 1981 (Stn BSS 118). Paratypes, type locality, NMVF50023-8, AMW198697-9, BMNHZB1984.49-51, USNM097291-3. Bass Strait E of King Island (39°43.7'S 144°46.7'E), 53 m, fine sand (Stn BSS 129 trawl), NMVF50029 (early epitoke). Additional material, Bass Strait—Stn BSS 56 DN, NMVF50175 (3 specimens); Stn BSS 112 SEB, NMVF50176; Stn BSS 119 SEB, NMVF50177 (6 specimens); Stn BSS 128 trawl, NMVF50178-9; Stn BSS 171 SEB, NMVF50180 (2 specimens); Stn BSS 171 TAM, NMVF50181 (14 specimens); widespread western Bass Strait Stns BSS 55, 57, 75, 77, 82, 107, 112, 113, 116, 118, 120, 127, 129, 155, 182, 183, 193, 196, 198, 199, 200, 201, 203, 204, 205 (NMV unregistered, total of about 170 specimens). Tasman Sea—Taupo Seamount (Guyot), 33°14'S, 156°08'5"E, 137 m, AMW198700 (7 specimens).

DESCRIPTION: Holotype an anterior fragment of 48 setigers, 22 mm length, 3 mm maximum body width. Colour in alcohol pale yellow brown with no obvious markings or pigmentation. Prostomial width slightly exceeds length. Two pairs of dark red eyes shallowly embedded, anterior pair slightly larger and slightly further apart. One pair of dorsoventrally compressed palps with palpostyles. One pair of antennae about half length of prostomium. Four pairs of tentacular cirri, faintly annulated, longest extending to setiger 4. Jaws stout, dark brown, with 6 teeth. Pharynx with pale brown conical paragnaths on both rings, arranged as follows: I=0; II=9, 6 in 2 crescent shaped rows; III=1; IV=15, 12; V=0; VI=2, 2 in a transverse row; VII-VIII=26 large and small cones in 2 rows.

Notopodia with two approximately equal lobes, smaller presetal lobe also present on setigers 8-20. Dorsal cirrus about 1.5 times length of dorsal notopodial lobe, becoming 2-2.5 times on posterior setigers. Notopodia thicker on anterior setigers, becoming elongate posteriorly. Neuropodia with two lobes, approximately equal on anterior setigers, ventral lobe becoming reduced posteriorly. Digitiform postsetal process present in neuropodia of anterior 12 setigers. Ventral cirrus basally attached, approximately half length of neuropodium on anterior setigers, becoming almost equal in length to neuropodium on posterior setigers (Fig. 2a,b). Notosetae all homogomph spinigers after setiger 2 (setigers 1 and 2 uniramous). Neurosetae

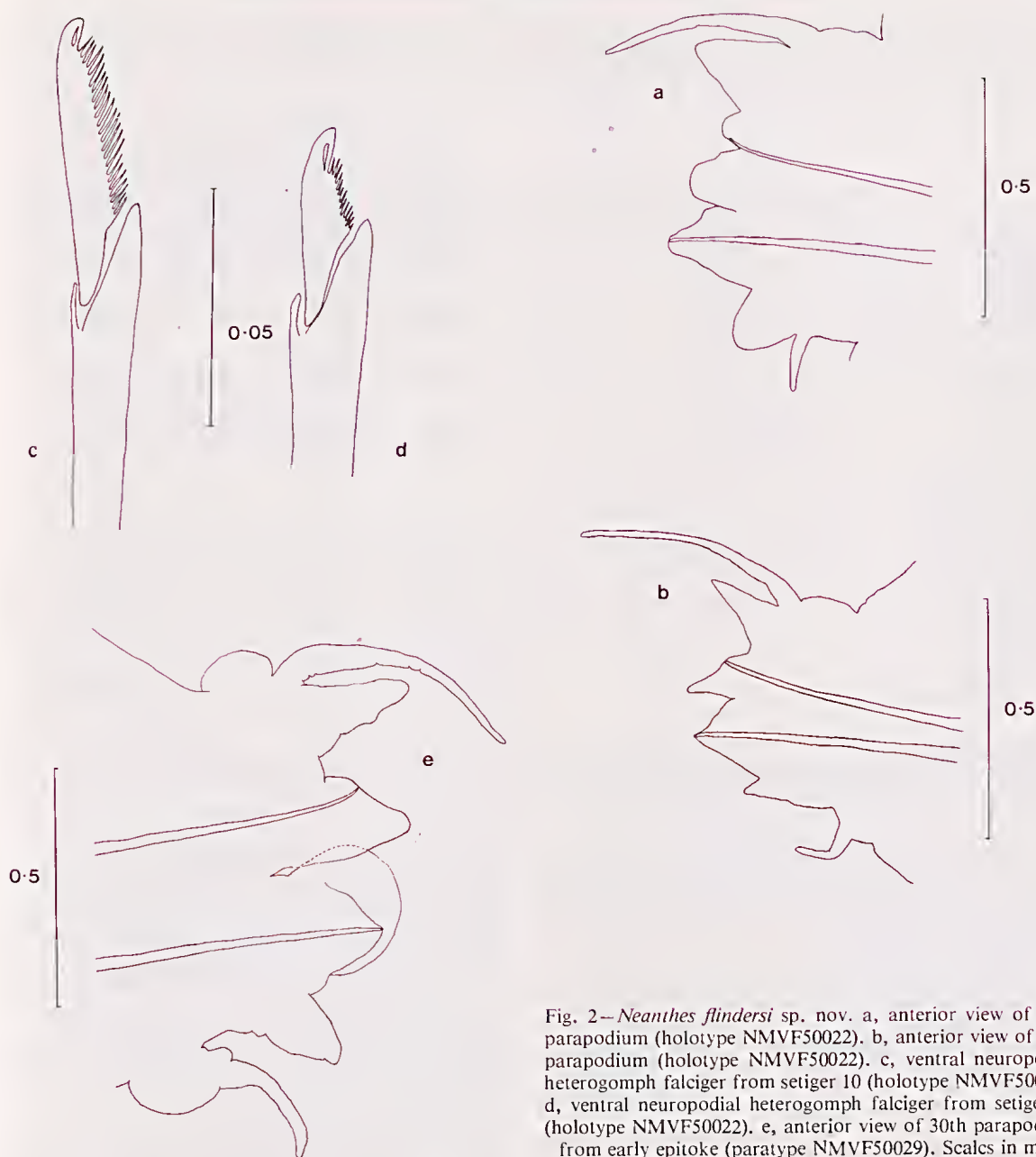


Fig. 2—*Neanthes flindersi* sp. nov. a, anterior view of 10th parapodium (holotype NMVF50022). b, anterior view of 47th parapodium (holotype NMVF50022). c, ventral neuropodial heterogomph falciger from setiger 10 (holotype NMVF50022). d, ventral neuropodial heterogomph falciger from setiger 47 (holotype NMVF50022). e, anterior view of 30th parapodium from early epitoke (paratype NMVF50029). Scales in mm.

heterogomph falcigers and homogomph spinigers in dorsal fascicle from setiger 1, ventral fascicle with homogomph spinigers and heterogomph falcigers (Fig. 2c, d) throughout. Heterogomph spinigers also present in ventral neuropodial fascicle of 6 anterior setigers but are absent posteriorly.

VARIATION: Variation not described for the holotype based on 14 paratypes (anterior fragments, size range 23 setigers, 5 mm length, 1 mm width, to 42 setigers, 21 mm length, 2.5 mm width; one entire specimen, NMVF50026, 58 setigers, 16 mm length, 1.5 mm width)

and on 23 additional specimens from material listed above (entire specimens, size range 23 setigers, 6 mm length, 1 mm width, to 50 setigers, 23 mm length, 3 mm width). No obvious markings or pigmentation. Tentacular cirri faintly annulated, longest extending to setiger 2-7, usually 4-5. Pharynx with pale brown conical paragnaths on both rings, arranged as follows: I=0; II=4-12; III=0-2 (usually 1); IV=6-21; V=0; VI=1-3 in a short transverse row; VII-VIII=16-30 in 2 rows of large and small cones.

Specimens >2 mm width with presetal notopodial

TABLE 3

Neanthes GROUP IIB 1 (PART; AFTER FAUCHALD 1972). COMPARISON OF SPECIES LACKING FUSED FALCIGERS, WITH FEWER THAN 20 PARAGNATHS ON AREA III, WITH PARAGNATHS IN TRANSVERSE ROW(S) ON AREA VI AND A BAND OF 1-3 ROWS ON AREAS VII-VIII.

	Area I	Area III	Area V	Area VI	Area VII-VIII	Presetal (3rd) notopodial lobe (anterior)	Postsetal (3rd) neuropodial lobe (setigers)	Source of data
<i>N. agulhana</i> Day 1963a	0	5-6	0	2-4	3-5 (1 R)	present	absent	Day 1963a
<i>N. biseriata</i> Hutchings & Turvey 1982	2-8	20-34	9-19	5-12 (2 R)	66-115 (2-3 R)	present	present	Hutchings & Turvey 1982; this study
<i>N. dawydovi</i> (Fauvel 1937)	0	4-7	0	2-3 (1 R)	3-5 (1 R)	absent	absent	Fauvel 1937
<i>N. flindersi</i> sp. nov.	0	0-2	0	1-3	16-30 (2 R)	present	present	this study
<i>N. heteroculata</i> (Hartmann-Schröder 1981)	0	7-12	0	2	17 (2 R)	absent	present	Hartmann-Schröder 1981
<i>N. kerguelensis</i> (McIntosh 1885)	0-1	0-14	0	0-1*	0-7† (1 R)	present	present	this study
<i>N. maculata</i> Wu Baoling & Sun Ruiping 1981	1	6-8	1	3-4 (1 R)	7 (1 R)	absent	absent	Wu Baoling & Sun Ruiping 1981
<i>N. uniseriata</i> Hutchings & Turvey 1982	2-6	4-24	4-9	3-6 (1 R)	30-59 (2-3 R)	present	present	Hutchings & Turvey 1982; this study

Explanation of abbreviations: R = suffix for number of transverse rows of paragnaths; * rarely 2-3 unilaterally; † rarely up to 12 on large specimens (see text).

lobe on about setigers 9-19 and also with neuropodial digitiform postsetal process on anterior 15-25 setigers. Heterogomph spinigers are present in the ventral fascicle of neurosetae anteriorly but are lost after setigers 3-14.

Anal cirri extend back 6-9 setigers.

Immature epitoke a gravid female (entire specimen, 72 setigers, 55 mm length, 3.5 mm width, NMVF50029) with paragnaths and setae as for atokous specimens. Eyes large, dark red. Dorsal and ventral cirri inflated basally on setigers 1-7. Epitokous parapodial modifications from setiger 17. Tubercles appearing at base of dorsal and ventral cirri, neuropodial postsetal digitiform process becoming lamellar (Fig. 2e).

REMARKS: *Neanthes flindersi* belongs to Fauchald's (1972) Group IIB 1. Within this group only 7 species have been described which, like *N. flindersi*, have fewer than 20 paragnaths on Area III, a transverse series on VI and a band of 2 rows on VII-VIII. Of the species listed in Table 3, *N. agulhana* Day 1963a most closely resembles *N. flindersi* but it may be distinguished by a pigmented band and spots on the anterior dorsum and by dorsal cirri becoming shorter on posterior setigers; *N. flindersi* is not pigmented and has dorsal cirri becoming longer posteriorly.

Among the species of *Neanthes* known from southern Australia, *N. flindersi* is most similar to *N.*

kerguelensis (McIntosh 1885) but can be distinguished from this and all known local species using the key. *N. flindersi* and *N. kerguelensis* also appear to differ in the distribution of heterogomph spinigers in the ventral neuropodial fascicle (see discussion of *N. kerguelensis*) but the variability of this potential taxonomic character is not yet fully understood.

ETYMOLOGY: *Neanthes flindersi* is named after Matthew Flinders who explored and charted much of the Australian coast.

DISTRIBUTION: Widespread western Bass Strait, one record eastern Bass Strait, one record from a seamount in the Tasman Sea. Known only from southeastern Australia.

HABITAT: Mostly carbonate sediments, 20-137 m.

Neanthes kerguelensis (McIntosh 1885)

Fig. 3

1885 *Nereis kerguelensis* McIntosh, p. 225, pl. 35, figs 10-12, pl. 16a, figs 17, 18.

1897 *Nereis kerguelensis* McIntosh; Ehlers, p. 65, figs 81-93.

1901a *Nereis kerguelensis* McIntosh; Ehlers, p. 260.

1901b *Nereis kerguelensis* McIntosh; Ehlers, p. 105.

1906 *Nereis kerguelensis* McIntosh; Gravier, p. 29.

- 1907 *Nereis kerguelensis* McIntosh; Ehlers, p. 11.
 1911 *Nereis kerguelensis* McIntosh; Gravier, p. 76.
 1913 *Nereis kerguelensis* var. *oligodonta* Augener, p. 164.
 1916 *Nereis kerguelensis* McIntosh; Benham, p. 122.
 1916 *Nereis kerguelensis* McIntosh; Fauvel, p. 433.
 1917 *Nereis kerguelensis* McIntosh; Fauvel, p. 203.
 1924 *Nereis kerguelensis* McIntosh; Augener, p. 330.
 1927a *Nereis kerguelensis* McIntosh; Augener, p. 134.
 1927b *Nereis kerguelensis* McIntosh; Augener, p. 346.
 1954 *Neanthes kerguelensis* (McIntosh); Hartman, p. 30.
 1967 *Neanthes kerguelensis* (McIntosh); Hartman, p. 64.
 1971 *Platynereis australis* (Schmarda); Knox & Cameron, p. 28 (partim.).
 1980 *Neanthes* sp. Dorsey and Synnot, p. 158.
 1982 *Neanthes kerguelensis* (McIntosh); Hutchings & Turvey, p. 113.

MATERIAL EXAMINED: W.A.—Point Peron, Rottnest Island, AMW18566; 3 mile reef, off Perth, 10.5 m, AMW18492; Fremantle, WAM94-84 (3 specimens).

S.A.—Penneshaw Jetty, Kangaroo Island, AMW18584; Rapid Bay, AMW18376 (5 specimens).

Tasmania—16 km N of Circular Head, AME6310 (2 specimens) (examined by Benham 1916); Pegleg Cove, Deal Island, 10-12 m, NMVF50028; Cape Sorell, AMW3661 (3 specimens); Pilot Bay, Cape Sorell, NMVF50047 (2 specimens).

Macquarie Island—Macquarie Island, AMW753.

Bass Strait—Stn BSS 77 GSM, NMVF50182, Stn BSS 117 SEB, NMVF50183 (2 specimens); Stn BSS 156 SEB, NMVF50184; Stn BSS 191 DR, NMVF50185; Stn BSS 201 SEB, NMVF50186 (15 specimens). Additional material, NMV unregistered: Stns BSS 72, 73, 77, 107-109, 112-113, 116, 117, 119, 127, 128, 131-133, 137-139, 152, 154, 156-158, 163, 171, 173, 182, 187, 188, 190, 191, 194, 197-201, 203-205, 209, 212 (total of approximately 130 specimens).

Victoria—Grey Point, Lorne, NMVF50031 (2 specimens); Aireys Inlet, NMVF50046; Black Rock, Connewarre, NMVF50134-5 (3 specimens) (*Neanthes* sp. of Dorsey & Synnot 1980); Port Phillip Survey Area 59 Stn 24, NMVG1640 (*Platynereis australis* of Knox & Cameron 1971); Port Phillip Bay, Sandringham Breakwater, NMVF50045; Merricks, Western Port, NMVF50030; Cape Woolamai, 30 m deep, NMVF50044 (2 specimens); Kilcunda, NMVF50043; W of Eagles Nest, NMVF50041 (2 specimens); near Eagles Nest, NMVF50042; Corner Inlet, 2 km S Sunday Island, 9 m; coll. 22 Nov. 1983, male epitoke, NMVF50187.

DESCRIPTION: Size range 35 setigers, 5 mm length, less than 1 mm width (entire specimen) to 32 setigers, 34 mm length, 5 mm width (anterior fragment). Tentacular cirri extending 4-8 setigers. Pharynx with conical to domed paragnaths sometimes faint or fused into an irregular mass. Paragnaths arranged as follows: I=0, rarely 1; II=3-18; III=0-14, usually 0-4; IV=4-26; V=0; VI=0-1 (2-3 on one side only in 3 specimens from

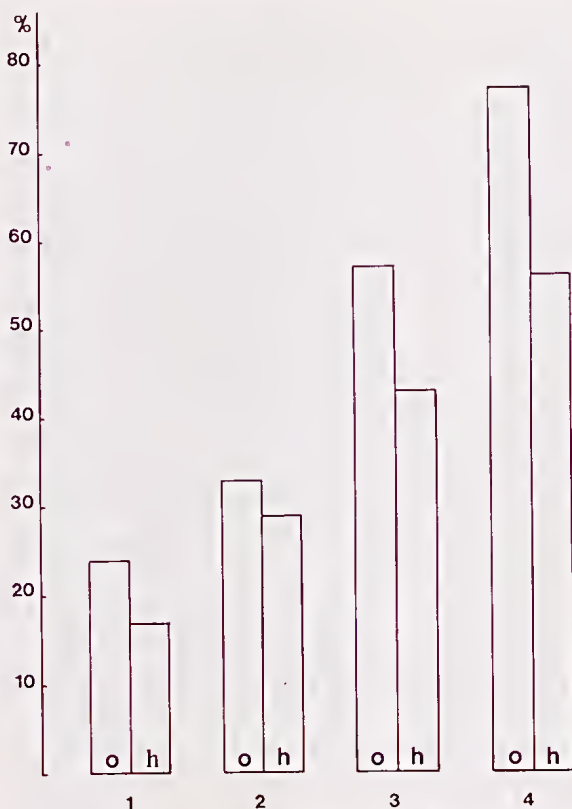


Fig. 3—*Neanthes kerguelensis* (McIntosh 1885). Frequency histogram showing percentage presence of oral ring paragnaths (o) and heterogomph spinigers (h) in 4 size classes. 1 ≤ 1.5 mm wide, n=41; 2 = 2, 2.5 mm wide, n=21; 3 = 3, 3.5 mm wide, n=14; 4 = 4-6 mm wide, n=9. Widths excluding parapodia, measured to nearest 0.5 mm.

Kangaroo Island, S.A., AMW18377); VII-VIII=0-7 (12 on one very large specimen, 6 mm wide, NMVF50030).

Notopodia with two lobes throughout, specimens wider than 1 mm with presetal notopodial lobe on at least setigers 9-14 (up to setigers 4-28 on specimens > 4 mm width). Dorsal cirrus approximately 1 to 1.5 times length of dorsal notopodial lobe, becoming 1.5 to 2 times length on posterior setigers. Neuropodia with two lobes throughout, specimens wider than about 1 mm with digitiform postsetal process on anterior 20-30 setigers, reducing in size posteriorly. Ventral neuropodial lobe slightly reduced posteriorly, ventral cirrus basally attached, approximately ¾ length of neuropodium throughout. Notosetae homogomph spinigers. Dorsal fascicle of neurosetae heterogomph falcigers and homogomph spinigers from setiger 1, ventral fascicle with homogomph spinigers and heterogomph falcigers throughout. Heterogomph spinigers may also be present in the ventral neuropodium in a variable number of anterior setigers but are absent at setiger 8 and all posterior setigers.

The only male epitoke available (NMVF50187) had modified parapodia commencing at setiger 15 but agrees

in all other respects with the description of male and female epitokes given by Ehlers (1897, p. 65, pl. 4, fig. 81-93).

REMARKS: The Southern Hemisphere synonymies included here indicate considerable variability in the number of oral ring paragnaths. The original description (McIntosh 1885) gives an oral ring paragnath formula of $V=0$, $V1=1$ on each side, $VII=VIII=5-6$. Augener (1913) described var. *oligodonta* from Western Australia with $V1=1$, $VII-VIII=3$ on the oral ring. He later examined material from New Zealand and southeastern Australia (Augener 1924b, 1927a) which also had few or no oral ring paragnaths and noted that specimens from warmer seas tended to a reduction in numbers of paragnaths on 1, III and the oral ring compared with Antarctic and sub-Antarctic material. Hartman (1954) recorded an oral ring formula of $V=0$, $V1=1$, $VII-VIII=9$ for South Australian material and Hutchings and Turvey (1982) recorded $V=0$, occasionally 1, $V1=0$, $VII-VIII=0-4$ and noted that some individuals were lacking or had very pale oral ring paragnaths.

In this study a detailed examination was made of variation in setae and paragnaths in 85 specimens from a variety of habitats in the Bass Strait region. The size of animals examined ranged from less than 1 mm to 6 mm wide although about half the sample was less than about 1.5 mm wide. Figure 3 presents percentage frequency of occurrence of oral ring paragnaths and heterogomph spinigers as a function of size class and shows that the presence of these two characters is related to the size of the worm. Some of the observed variation is however not explained by size and appears to be unrelated to other morphological characters or to habitat.

The variability observed within *N. kerguelensis* in this study from a restricted area exceeds the variability observed by earlier workers in the Southern Hemisphere and suggests problems in distinguishing material from more distant localities. Hartmann-Schröder (1981) gave a partial Northern Hemisphere synonymy, a distribution from Antarctica to north and central Atlantic and Mediterranean and habitat range from intertidal to 5 000 m. Further work is required to examine variation within and between populations from these widely separated localities and habitats.

The variability observed in *N. kerguelensis* may also present problems in distinguishing that species from *N. flindersi*. Juvenile specimens (<1 mm width) will be indeterminate unless absence of heterogomph spinigers from the anterior 6-10 setigers can be determined with certainty. Heterogomph spinigers are always present anteriorly in *N. flindersi* but are absent in some specimens of *N. kerguelensis*. Specific determinations based on oral ring paragnath counts should be possible in all material exceeding 1 mm in width.

DISTRIBUTION: Southwestern Western Australia, South Australia, Tasmania, Victoria, New South Wales. Widely recorded in Northern and Southern Hemispheres.

HABITAT: Associated with fouling communities, inter-

tidal in rocks and sand on sheltered and exposed coasts, soft bottom benthos to 115 m deep.

Neanthes succinea (Leuckart 1847)

Fig. 4

- 1847 *Nereis succinea* Leuckart, p. 154, pl. 2, figs 9, 11.
- 1934 *Nereis oxypoda* (Marenzeller); Monro, p. 362. (*partim*.)
- 1938 *Nereis oxypoda* (Marenzeller); Monro, p. 614, figs 1-5.
- 1963 *Nereis* (*Neanthes*) *succinea* Leuckart; Pettibone, p. 165, figs 44a-c, 45a-d.
- 1967 *Nereis* (*Neanthes*) *succinea* Leuckart; Day, p. 321, fig. 14.9a-c.
- 1972 *Neanthes succinea* (Leuckart); Imajima, p. 108, figs 32a-k, 37.
- 1984 *Neanthes oxypoda* (Marenzeller); Hutchings & Murray, p. 37.

MATERIAL EXAMINED: W.A.—Crawley Bay, Swan River, immature female epitoke, gravid, coll. summer 1930, BMNHZK 1938.10.31.7; Swan River, immature female epitoke, gravid, coll. 17 Aug. 1935, BMNHZK 1938.10.31.8; Pelican Point, Swan River, 3 specimens, including 1 immature female epitoke, gravid, coll. 12 April 1930, BMNHZK 1938.10.31.9-10 (material identified as *Nereis oxypoda* by Monro 1938).

Victoria—Hobsons Bay, PPBES: Stn 128, NMVF50084, F50085 (6 specimens); Stn 130, NMVF50086, F50087; Stn 132, NMVF50088; Stn 136, 3, NMVF50089; Stn 134, NMVF50090 (immature epitoke), Hobsons Bay, Yarra River at Westgate Bridge, coll. 10 April, 1984, 9 m, NMVF50128; Yarra River, Newport Powerhouse site, many, male and female epitokes, NMVG1109; Port Phillip Bay off Yarra River mouth coll. 20 Oct. 1978, 1, sub-epitoke, NMVF50083; Maribyrnong River, at Sims Street, coll. 4 Mar. 1981, 1, sub-epitoke, NMVF50129.

N.S.W.—Port Hacking: Stn 630, AMW195244 (2 specimens); Stn 631, AMW195222; Stn 641, AMW195305 (2 specimens). Hawkesbury River: Stn D2-2, AMW196461; Stn D2-3, AMW196462 (2 specimens); Stn D4-3, AMW196463. Lake Macquarie, *Zostera* beds, AMW17830. (Full locality data given by Hutchings & Murray 1984).

China—Amoy, coll. T. Y. Chen, immature female epitoke, gravid, BMNHZK 1933.3.2.40 (1 of 3 specimens identified as *Nereis oxypoda* by Monro 1934, see below).

U.S.A.—Sippiswissett, Mass. coll. 25 Jan. 1953, M. H. Pettibone, USNM27799 (23 specimens).

Canada—Off Sheldrake Island, Miramichi River, Nova Scotia, coll. 28 July 1952, USNM35807 (9 epitokes).

Netherlands—E of Schokland, Zuiderzee, coll. 17 Aug. 1905, USNM27897 (3 specimens).

W. Germany—Ems River, freshwater, coll. 1954/55, HZMP13065, P13067, V13071 (30 specimens); Helgoland, HZMP16369 (2 specimens); Kugelbake, Cuxhaven, HZMV10925 (2 specimens); Americhafen, Cuxhaven, HZMV9984, V10693 (4 specimens).

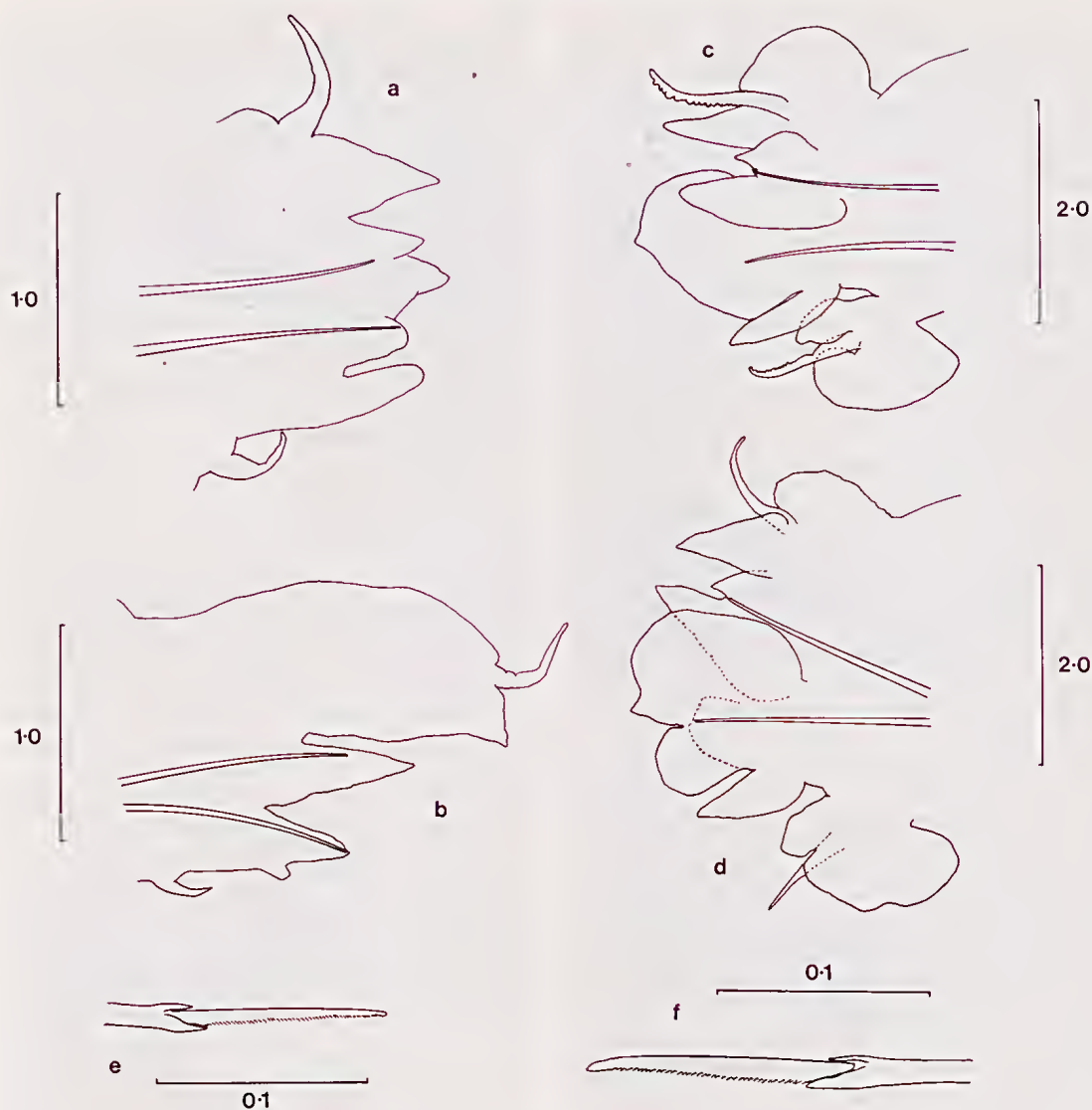


Fig. 4—*Neanthes succinea* (Leuckart 1847) a, posterior view of 10th parapodium (NMVF50087). b, anterior view of 39th parapodium (NMVF50087). c, anterior view of 35th parapodium from immature male epitoke (NMVG1109, part). d, posterior view of 30th parapodium from immature female epitoke (NMVG1109, part). e, ventral neuropodial heterogomph falciger, setiger 10 (atoke, NMVF50087). f, ventral neuropodial heterogomph falciger, setiger 7 (immature male epitoke, NMVG1109, part). Scales in mm.

DESCRIPTION: Description based solely on 28 specimens selected from the Australian material listed above. Size range of material examined 30 setigers, 5 mm long, less than 1 mm wide (entire specimens) to 89 setigers, 155 mm long, 8 mm wide (anterior fragment). Prostomial length slightly exceeds width. Two pairs of red eyes. One pair of palps with small palpostyles, one pair of antennae about $\frac{1}{3}$ as long as prostomium. Four pairs of tentacular cirri, longest extending 3-6 setigers posteriorly. Jaws translucent brown with about 5-6 teeth. Pharynx with conical paragnaths on all Areas, arranged as follows: I=0-5 (usually 2-3) in longitudinal

series; II=7-23, 2 rows in a crescent; III=2-42, usually 20-30 in an oval group; IV=13-34 in 2-3 curved rows, tapering to 1 row close to the base of the maxillae; V=0-4, usually 2-3 in a triangle; VI=6-14 in a roughly circular group; VII-VIII=36-62 in 2-3 rows.

Notopodia anteriorly with three triangular lobes and basally attached dorsal cirrus, all approximately equal in length. Dorsal lobe becoming expanded posteriorly, lamellar in form with dorsal cirrus attached subdistally (dorsal cirrus distally attached on posterior most segments). Median lobe becoming reduced posteriorly, may be absent from about setiger 25 on specimens

<2 mm body width but persisting to setiger 40 to 50 at least on larger specimens. Neuropodia with two triangular lobes, approximately equal in length throughout and prominent postsetal lobe of approximately equal length, decreasing slightly on posterior-most setigers (Fig. 4a, b). Notosetae homogomph spinigers. Dorsal fascicle of neurosetae homogomph spinigers and heterogomph falcigers, ventral fascicle of neurosetae heterogomph spinigers and falcigers. The appendages of the heterogomph falcigers are distinctively long and narrow with blunt rounded tips (Fig. 4e, f). Several immature epitokes with homogomph and heterogomph spinigers throughout, falcigers absent. Natatory setae present only in advanced epitokes (NMVG1109). Anal cirri extend back over 7-14 setigers.

Male epitokes with dorsal cirri inflated on setigers 1-7, ventral cirri inflated on setigers 1-5. Epitokous parapodia from setiger 15; ventral surface of dorsal cirri and dorsal surface of ventral cirri crenulate, inflated lobes at the bases of both cirri. Median notopodial lobe reduced posteriorly, dorsal and ventral notopodial lobes elongate, lamellar, median notopodial lobe reduced posteriorly. Dorsal neuropodial lobe inflated, discoid, ventral neuropodial lobe digitiform (Fig. 4c). Posterior most setigers approximately as for atokes: dorsal notopodial lobe an elongate triangle, remaining lobes shorter triangles.

Female epitokes with dorsal cirri inflated on setigers 1-5, ventral cirri inflated on setigers 1-3. Epitokous parapodia appear variably from setiger 16-20, usually 18-20. Dorsal and ventral cirri smooth throughout, a single dorsally inflated lobe at the base of the dorsal cirri, a pair of inflated lobes at the base of the ventral cirri. Median notopodial lobe reduced posteriorly, remaining notopodial lobes elongate triangles. Dorsal neuropodial lobe divided along the line of the neuro-aciculum into unequal discoid lobes, the dorsal lobe being the larger. Ventral neuropodial lobe digitiform (Fig. 4d). Posteriormost setigers approximately as for atokes.

REMARKS: The type of *N. succinea* is in poor condition (G. Hartmann-Schröder, pers. comm.). However, material has been examined from a range of Northern Hemisphere localities including the type locality (Helgoland and Cuxhaven, German North Sea). The Australian material described here agrees with the Northern Hemisphere material in every detail except for the variability observed in the paragnath counts of Area III: several Australian specimens, including 9 specimens from N.S.W. and 5 specimens from W.A. have only 2-4 paragnaths here, compared with 20-30 on most Victorian specimens and on all Northern Hemisphere specimens examined. This character state does not appear to be related to size of specimen or to any other morphological character and is considered here as part of the normal intraspecific variation of *N. succinea* (in this study *N. bassi* and *N. kerguelensis* were also found to exhibit considerable variability in paragnath counts on Area III).

Two Australian records of *Neanthes* (*Nectoneanthes*) *oxypoda* (Marenzeller 1879) are included above in

the synonymy of *N. succinea*. This material (Monro 1938, Hutchings & Murray 1984) includes epitokes at various stages of development; these specimens differ from atokous *N. succinea* only in the expected epitokal modifications of parapodia and setae (as noted in the description above, these modifications include the loss of neuropodial falcigers in some immature epitokes). Paragnath counts and unmodified parapodia from the natatory region do not appear to vary significantly with the development of epitoky and several immature epitokes retain a few neuropodial falcigers, the form of which is distinctive (Fig. 4f). The epitokes examined here also agree with the detailed description given by Pettibone (1963) of epitokous modifications in *N. succinea* from N. America and all Australian records are thus referred to this species.

Monro (1934, p. 362) reported 3 specimens of *N. oxypoda* from Amoy, China, and noted that: 'The specimen collected by Chen corresponds exactly to Marenzeller's account. The other two show a marked variation in the arrangement of the paragnaths.' The specimen collected by Chen (BMNHZK 1933.3.2.40) agrees in every respect with the *N. succinea* epitokes examined in this study and is included in the above synonymy. The remaining 2 specimens (BMNHZK 1926.4.27.22-23) differ from *N. succinea* in that a continuous band of paragnaths 8-10 deep is present through Areas V-VIII of the oral ring. These specimens appear to agree in all other respects with the *N. succinea* epitokes examined in this study but in view of the substantial deviation from the paragnath counts of that species I prefer to retain this distinct form as *Neanthes* (*Nectoneanthes*) *oxypoda* var. A third specimen of *N. oxypoda* var. examined in this study, a gravid immature female epitoke (USNM22240), appears to have been split from Chen's collection before its examination by Monro; labels of both specimens carry the information 'Amoy, China, coll. T. Y. Chen, No. 27'. Imaijima (1972) has also described and figured this form (as *Nectoneanthes oxypoda*) from 7 localities in southern Japan.

In summary, the above findings show that published records of *Neanthes* (*Nectoneanthes*) *oxypoda* from Australia, China and Japan confuse two distinct forms. One form, designated here as *N. oxypoda* var., is known only from epitokes from China and Japan and is probably an undescribed species. Atokous material will be required before this form can be given an accurate generic placement. Monro (1934), and probably all remaining records including the original description of *N. oxypoda* (Marenzeller 1879), appear to describe epitokes of *N. succinea*. If Marenzeller's type material can be located and agrees with his original description then *N. oxypoda* would become a junior synonym of *N. succinea*.

The genus *Nectoneanthes* Imaijima 1972 was erected for species of *Neanthes* which lack neuropodial falcigers. Four species are currently placed in *Nectoneanthes*: *N. alatopalpis* (Wesenberg-Lund 1949), *N. imajimai* Imaijima 1972, *N. oxypoda* (Marenzeller 1879, type species and *N. multignatha* Wu Boaling & Sun Ruiping 1981. *Nectoneanthes* differs from *Neanthes* only in the lack of neuropodial falcigers and the expan-

sion of the superior notopodial lobe on median setigers, characters which are associated with the development of epitoke. Group 1 of Fauchald's (1972) subdivision of *Neanthes* was also created for species lacking falcigers and contains four species which were not included in *Nectoneanthes* by Imaijima (1972). At least one species in Fauchald's Group I, *N. virens* (Sars 1835) does possess neuropodial falcigers although they may be lost in adult worms (Pettibone 1963). Both *Nectoneanthes* Imaijima 1972 and *Neanthes* Group 1 (Fauchald 1972) appear to be based on inadequate material and require reappraisal. Neither group is represented in Australian material.

I cite Leuckart 1847 as author of *N. succinea*, not Frey & Leuckart 1847, as is widely cited elsewhere. This interpretation is due to Mr. A. Muir (pers. comm.) who drew my attention to the relevant passage of the introduction to Frey and Leuckart, 1847 which states (in translation from the German: '... the last paper on the fauna of Helgoland ... is exclusively a property of Dr Leuckart'.

DISTRIBUTION: Western Australia (Swan River), Victoria (Yarra and Maribyrnong Rivers), New South Wales (Port Hacking, Hawkesbury River, and Lake Macquarie). Widely recorded in Northern and Southern Hemispheres.

HABITAT: Appears to be restricted to estuaries (in Australia).

Neanthes uniseriata Hutchings & Turvey 1982

1982 *Neanthes uniseriata* Hutchings & Turvey, p. 113, fig. 8a-c, table 8.

MATERIAL EXAMINED: S.A.—Victor Harbour (18A), 14 paratypes, AMW18433; Cape de Couedic, Kangaroo Island, 50 paratypes, AMW18432. (full locality data given by Hutchings & Turvey 1982).

Vic.—Anglesea Reef, coll. 16 Oct. 1976, NMVF50078 (2 specimens); Somers, Western Port, NMVF50073; Shoreham Reef, Western Port, coll. Jan. 1967, NMVF50074; Merricks, Western Port, coll. 1969, NMVF50075; Cat Bay, Phillip Island, coll. 18 Feb. 1978, NMVF50076 (40 specimens); Sunderlands Bay, Phillip Island, coll. 3 July 1979, NMVF50077; Kilcunda, coll. Jan. 1966, NMVF50071, F50072 (10 specimens).

DESCRIPTION: Size range of material examined 41 setigers, 5 mm long, <1 mm wide to 76 setigers, 31 mm long, 3 mm wide (entire specimens). Pharynx with conical paragnaths on all Areas, some specimens with a few short bars also present on Area IV, arranged as follows (counts based on 30 specimens, including 9 from the type series): I=2-6, usually 4-5; II=3-13; III=4-24, usually 11-22; IV=8-26 cones and 0-3 short bars; V=4-9, usually 5-7; VI=3-6 in a single arc occasionally including 1 or 2 behind; VII-VIII=30-59 large cones only.

Notosetae all homogomph spinigers. Neurosetae heterogomph falcigers and homogomph spinigers throughout in the dorsal fascicle and heterogomph falcigers and heterogomph spinigers in the ventral fascicle.

REMARKS: The Victorian material agrees with the description given by Hutchings and Turvey (1982) and with the type series from South Australia. The present author disagrees with Hutchings and Turvey on the interpretation of the borders of Area VI of the pharynx and thus there are slight differences in paragnath formulae from those given by Hutchings and Turvey. As with *N. biseriata* counts for Area VI only include those paragnaths which form the single arc which characterises *N. uniseriata* even though part of the ventral band of paragnaths and some paragnaths on Area V may be interpreted as extending into Area VI.

DISTRIBUTION: South Australia and Victoria. Known only from southeastern Australia.

HABITAT: Intertidal in algae and in rocks and sand.

Neanthes vaalii Kinberg 1866

1866 *Neanthes vaalii* Kinberg, p. 171.

1981 *Neanthes vaalii* Kinberg; Hartmann-Schröder, p. 42, figs 88-93.

1982 *Neanthes vaalii* Kinberg; Hutchings & Turvey, p. 116.

1984 *Neanthes vaalii* Kinberg; Hutchings & Murray, p. 40.

MATERIAL EXAMINED: W.A.—King River, Albany, coll. 6 Mar. 1971, WAM49-74 (part); Walpole Inlet, Walpole, coll. 5-10 Aug. 1973, WAM97-84 (many specimens).

S.A.—Waldegrave Island, coll. 25 Oct. 1973, AMW18490; Thevenard (nr. Ceduna), coll. 4 Feb. 1970, AMW4341 (3 specimens).

Tasmania—Derwent River, coll. 4 May 1982, NMVF50039 (2 specimens); Huon River Site 12, coll. Feb. 1976, AMW11076; Huon River Site 14, coll. 5 Feb. 1976, AMW11096 (2 specimens).

Victoria—Port Phillip Bay, Ricketts Point, coll. Feb. 1964, NMVF50038 (5 specimens); Western Port CPBS: Stn 000, NMVF50227 (34 specimens); Stn 02N, NMVF50228 (2 specimens); Stn 03N, NMVF50229 (13 specimens); Point Leo, coll. 18 Jan. 1969, NMVF50036; Hastings, coll. 1 Mar. 1962, NMVF50037 (epitoke); Corinella, coll. 8 Feb. 1969, NMVF50035 (3 specimens); Western Port Canons Creek, coll. 1 April 1970, NMVF50034; Corner Inlet, 3.5 km WSW of McLoughlans Beach, 2 m, 22 Nov. 1983, NMVF50188; S of Manns Beach, intertidal, 19 Nov. 1983, NMVF50189-90 (11 specimens); 1 km SE of Manns Beach, 0.5 m, 22 Nov. 1983, NMVF50191; 0.5 km W of Port Welshpool, intertidal, 20 Nov. 1983, NMVF50192; cove on N side Doughboy Island, 2 m, 24 Nov. 1983, NMVF50193; N end of Long Island, 0.1 m, 23 Nov. 1983, NMVF50194 (2 specimens); Gippsland Lakes GRES Stn 3073, NMVF50033 (2 specimens).

N.S.W.—Batemans Bay, coll. 10 Jan. 1970, NMVF50032.

DESCRIPTION: Size range 29 setigers, 5 mm length, <1 mm width (anterior fragment) to 89 setigers, 31 mm length, 3 mm width (entire specimen). Large specimens with even dark blue/brown pigmentation on anterior dorsum, smaller specimens pale. Tentacular cirri long,

longest extending 9-10 setigers. Pharynx with conical paragnaths on both rings and smooth bars also present on IV only. Paragnaths arranged as follows: I=1-4 (usually 2 or 3) in longitudinal series; II=7-17; III=19-28 often with 1 or 2 separate at each side; IV=16-33 cones and 1-4 smooth bars; V=3 in a triangle, rarely only 1 or 2; VI=3-5 in a compact group, rarely with fewer (0-2) on one side; VII-VIII=37-59 in 2-3 rows extending on to VI.

Notopodia with two lobes approximately equal in size throughout, large specimens also with presetal notopodial lobe on about setigers 6-20 (presetal lobe present on fewer setigers on smaller specimens and absent on specimens less than about 1.5 mm wide). Dorsal cirrus approximately twice length of notopodial lobes. Neuropodia with two lobes, ventral lobe slightly smaller. Digitiform postsetal process absent. Ventral cirrus extending to tip of ventral neuropodial lobe. No marked change in relative proportions of parapodial lobes on posterior segments. Notoetae homogomph spinigers. Neuroetae homogomph spinigers and heterogomph falcigers in dorsal fascicle in all setigers, heterogomph spinigers and heterogomph falcigers in ventral fascicle in all setigers.

Anal cirri extend back 4-8 setigers.

Male epitoke (NMVF50037) 102 setigers, fully mature. Eyes large, lacking pigment (in alcohol). Paragnaths as for atokous specimens. Dorsal cirri of anterior 7 setigers and ventral cirri of anterior 5 setigers basally inflated. Setigers 4-17 with presetal notopodial lobe. Parapodia showing epitokal modifications from setiger 18: ventral surface of dorsal cirri crenulate, expanded lamellar lobes dorsally at the base of the dorsal cirrus and ventrally at the base of the ventral cirrus, digitiform lobes situated medially at the base of each cirrus, large lamellar postsetal lobe in neuropodia. Specialised natatory setae present in all modified parapodia. Pygidium with an expanded rosette of many digitiform papillae. Anal cirri appear to be absent. Epitokous modifications agree with the descriptions given by Hartman (1954, p. 28, fig. 24). Hartmann-Schröder (1981, p. 42, figs 91, 92) described modifications of an immature epitoke.

REMARKS: The presence of smooth bar paragnaths in addition to cones on Area IV has not been reported for *N. vaalii* but was noted on all material examined in this study.

DISTRIBUTION: Temperate Australia from Geraldton, Western Australia to Careel Bay, New South Wales. Known only from Australia and New Zealand.

HABITAT: Sheltered coasts, associated with fouling communities, oysters, mussel clumps, under rocks, in *Zostera*; intertidal to 4 m deep.

Neanthes cricognatha and *N. kerguelensis* are cosmopolitan species or species complexes; both occur in a variety of habitats but in Australia they occur most commonly on the continental shelf of Bass Strait. Two new species described in this study also occur in Bass Strait; *N. bassi*, which is also recorded from Port Phillip Bay, and *N. flindersi*, which appears to be restricted to

the continental shelf. The *Neanthes* fauna of Bass Strait is thus qualitatively and quantitatively different from that of Port Phillip Bay and Western Port (Table 4).

Neanthes succinea is recorded here from Australia for the first time. This species is known from a variety of marine and estuarine habitats elsewhere in its range (Pettibone 1963) but in Australia it appears to be restricted to a few estuaries. Most of these localities are associated with international ports and it has been suggested that these records may represent accidental introductions (K. Fauchald pers. comm.).

Neanthes biseriata and *N. uniseriata* are closely related species which are usually collected from exposed rocky shores. Both species also occur at less exposed sites but are rarely collected with *N. vaalii*, which is widespread at sheltered localities and in seagrass.

ACKNOWLEDGEMENTS

I thank K. Fauchald (Smithsonian Institution, Washington), G. Hartmann-Schröder (Zoologisches Institut und Museum der Universität Hamburg), D. George and A. Muir (British Museum, London), P. Hutchings (Australian Museum, Sydney) and L. Marsh (Western Australian Museum, Perth) for advice, loan of material and assistance with literature. I also thank K. Fauchald and P. Hutchings for their constructive comments on earlier drafts of this paper and R. Synnot and S. Davies (Melbourne and Metropolitan Board of Works) for providing additional material of *Neanthes succinea*. I am particularly grateful for the encouragement and assistance of M. Gomon, C. C. Lu and G. Poore (Museum of Victoria) and P. Hutchings. This study was supported by a Marine Sciences and Technologies Grant.

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TABLE 4
SUMMARY OF ECOLOGICAL DATA FOR VICTORIAN SPECIES OF *Neanthes*

	Bass Strait benthos (BSS)	Port Phillip Bay benthos (PPBS)	Western Port benthos (CPBS)	Exposed rocky shores	Sheltered coast rock & seagrass
<i>N. bassi</i>	uncommon	uncommon	—	—	—
<i>N. biseriata</i>	—	—	—	common	uncommon
<i>N. cricognatha</i>	common	uncommon	common	uncommon	uncommon
<i>N. flindersi</i>	common	—	—	—	—
<i>N. kerguelensis</i>	common	—	—	uncommon	uncommon
<i>N. succinea</i>	—	common*	—	—	—
<i>N. uniseriata</i>	—	—	—	common	uncommon
<i>N. vaalii</i>	—	—	uncommon	—	common

Species are defined as common in benthic surveys if they occur at 10% or more of stations. Common for exposed and sheltered sites is based on qualitative records presented in this study.

* Yarra and Maribyrnong Rivers only.

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- c Dorsal lobes prolonged in posterior setigers
C Development of parapodial lobes unknown
- N. abyssorum* Hartman 1967: 63-4, pl. 16, fig. a, b. Bransfield Strait, Antarctica, ca. 2,500 m. Group IIB 1†.
- N. agnesiae* (Augener 1918: 194-7, pl. 3, figs 69-71, pl. 4 figs 76-7), as *Nereis (Alitta) agnesiae*. Southwest Africa. Group I.
- N. agulhana* (Day 1963a: 406-7, textfig. 6d-j), as *Nereis (Neanthes) agulhana*. South Africa. Group IIB 1.
- N. angusticollis* (Augener 1913: 145-9, pl. 2, fig. 14u, textfig. 13a-d), as *Nereis angusticollis*. Perth, Shark Bay, southwestern Australia. HOMONYM. Group IIB 1.
- N. arenaceodentata* (Moore 1903: 720-3, pl. 40, figs 1-10), as *Nereis arenaceodentata*. Massachusetts. Group IIB 1†.
- N. articulata* Knox, 1960: 121-2, figs 174-9. Chatham Is, New Zealand. Group IIB 2a.
- N. augeneri* (Gravier & Dantan 1934: 52-4, figs 12-13), as *Nereis (Neanthes) augeneri*. Annam. Group IIC.
- N. bassi* sp. nov., see above. Bass Strait, southern Australia. Group IIB 1†.
- N. belawanensis* (Pflugfelder 1933: 72-3, fig. 13), as *Nereis belawanensis*. Sumatra. Group IIB 1.
- N. biseriata* Hutchings & Turvey 1982: 108-110, fig. 6a-d. South Australia. Group IIB 1†.
- N. brandti* (Malmgren 1866: 183-4), as *Alitta brandti*. Siberia. Group IIB 2a. See also Hartman, 1968: 523.
- N. caudata* (delle Chiaje 1828, in Quatrefages 1865: 551)*, as *Spio caudatus*, Southern Europe. Group IIB 1. See also Fauvel, 1923: 347-8, fig. 135a-e.
- N. chilkaensis* (Southern 1921: 584-9, pl. 22, fig. a-r, textfig. 4a-c), as *Nereis (Nereis) chilkaensis*. Chilka Lake, India. Group IIB 1. See also Fauvel, 1923: 94-5.
- N. chingrighattensis* (Fauvel 1932: 90-1, fig. 14a-h), as *Nereis chingrighattensis*. Chingrighatta, India, Group 1.
- N. cortezi* Kudenov 1979: 118-20, fig. 2a-h. Gulf of California. Group IIB 2c.
- N. cricognatha* (Ehlers 1904: 29-30, pl. 4, fig. 3-7), as *Nereis cricognatha*. New Zealand. Group IIB 1†. See also this study.
- N. crucifera* (Grube 1878: 80-1, pl. 5, fig. 6), as *Nereis (Lycoris) crucifera*. Philippine Islands. Group IIB 2b.
- N. dawydovi* (Fauvel 1937: 297-9, fig. 1a-k), as *Nereis dawydovi*. Indo-China. Group IIB 1.
- N. donghaiensis* Wu Boaling & Sun Ruiping 1981: 215-6 (English summary), fig. 82a-c. Fukien, China. Group IIB 1†.
- N. diversicolor* (Müller 1776: 217), as *Nereis diversicolor*. Denmark. See *Hediste diversicolor*, fide Hartmann-Schröder 1971, Fauchald 1977a.
- N. flava* Wu Boaling & Sun Ruiping 1981: 218 (English summary), fig. 89a-1. Hopei, China. Group IIB 1†.
- N. flindersi* sp. nov. see above. Bass Strait, southern Australia. Group IIB 1†.
- N. fucata* (Savigny 1818: 210-1), as *Lycoris fucata*. Mediterranean Sea. Group IIB 2a.
- N. galetae* Fauchald 1977b: 26-7, fig. 6a-c. Panama. Group IIB 1.
- N. glandicincta* (Southern 1921: 589-93, pl. 23, fig 9a-1, textfig. 5a-c), as *Nereis (Nereis) glandicincta*. Calcutta, India. Group IIB 1. See also Fauvel 1932: 92-3.
- N. helenae* Kinberg 1866: 172. St. Helena Island. Incompletely known; may include *Neanthes nanciae*.
- N. heteroculata* Hartmann-Schröder 1981: 30-1, fig. 9-13. Bay of Biscay, 4 700 m. Group IIB 1.
- N. indica* (Kinberg 1866: 169), as *Nereis indica*. Group IIB 1. See also Willey 1905: 270-1; Fauvel 1932: 96.

APPENDIX

Species of *Neanthes* Kinberg 1866, with reference to original descriptions, type locality and grouping according to Fauchald (1972) (after Hartman 1959, 1965).

* denotes any reference that has not been seen in the original by me.

† denotes any Fauchald grouping that has been emended or is made for the first time on my authority.

The Fauchald grouping is repeated here:

I Falcigers absent

II Falcigers present (or presence or absence not known)

A Parapodial lobes with papillae

B Parapodial lobes smooth

1 Dorsal lobe of notopodia barely longer than the other parapodial lobes, usually triangular

2 Dorsal lobe of notopodia longer than the other lobes

a Dorsal lobes large thick or foliose

b Dorsal lobes slender, long in all setigers

- N. indica brunnea* Day 1957: 79-81, fig. 4h-n. Mozambique Is, South Africa. Group IIB 1.
- N. isolata* Hutchings & Turvey 1982: 111-3, fig. 7a-d. South Australia. Group IIB 1†.
- N. japonica* Izuka 1908: 294-305, textfig. 1a, c. Japan. Group IIB 2a. See also Izuka, 1912: 163-9, pl. 17, fig. 14-16, 18.
- N. kerguelensis* (McIntosh 1885: 225-7, pl. 35, fig. 10-12), as *Nereis kerguelensis*. Kerguelen Islands. Group IIB 1. See also this study.
- N. latipalpa* (Schmarda 1861: 104-5, pl. 31, fig. 244), as *Nereis latipalpa*. Capc of Good Hope. Group IIB 1†. See also Willey, 1904: 260-1, pl. 13 fig. 1-2a, b.
- N. larentukana* Grube 1881: 110-1, as *Nereis* (*Neanthes*) *Larentukana*. 'Larentuka.' Group IIB 2a.
- N. limnicola* (Johnson 1903: 205-22, pl. 16, 17), as *Nereis limnicola*, Lake Merced, California. Group IIB 1. Includes *Neanthes lighti* Hartman 1938: 80-2, fig. 1-4. See also Smith 1959: 349-50.
- N. macrocephala* (Hansen 1882: 13-4, pl. 4, fig. 29-33), as *Nereis macrocephala*. Brazil. Group IIB 1.
- N. maculata* Wu Boaling & Sun Ruiping 1981: 216-7 (English summary), fig. 83a-j. Canton, China. Group IIB 1†.
- N. mancorae* (Berkeley & Berkeley 1961: 656-7, fig. 1-4), as *Nereis* (*Neanthes*) *mancorae*. Peru. Group IIB 2c†.
- N. meggitti* (Monro 1931: 580-5, fig. 1-6), as *Nereis* (*Neanthes*) *meggitti*. Rangoon. Group IIB 1.
- N. mexicana* Fauchald 1972: 70-1, pl. 11, fig. a-d. Baja California, ca. 1900 m. Group 1.
- N. mossambica* (Day 1957: 77-8, 80, fig. 3e-l), as *Nereis* (*Neanthes*) *mossambica*. Mozambique Is. South Africa. Group IIB 2b.
- N. nanciae* (Day 1949: 445, fig. 4), as *Nereis nanciae*. St. Helena Island. Group IIB 2a. See also *Neanthes helenae*.
- N. nanhaiensis* Wu Boaling & Sun Ruiping 1981: 217-8 (English summary), fig. 86a-j. South China Sea. Group IIB 1†.
- N. noodti* Hartmann-Schröder 1962: 129-30, pl. 11, fig. 65-6, pl. 12, fig. 68, pl. 20, fig. 67. Peru. Group IIB 2c.
- N. papillosa* (Day 1963b: 360-2, fig. 2a-g), as *Nereis* (*Neanthes*) *papillosa*. W of Cape Town, South Africa. 2 745 m. Group IIA.
- N. pseudonoodti* Fauchald 1977b: 27-9, fig. 7a-d. Panama. Group IIB 2c.
- N. reducta* (Southern 1921: 593-5, pl. 21, fig. 7a-k, textfig. 6a-d.), as *Nereis* (*Nereis*) *reducta*. Chilka Lake, India. Group IIB 1.
- N. roosevelti* Hartman 1939: 11-13, fig. 2c-h. Galapagos Islands. Group IIB 1.
- N. sakhalinensis* (Okuda 1935: 54-7, fig. 1a-b, fig. 2a-c, fig. 3a-e), as *Nereis sakhalinensis*. Sakhalin Is, Japan. Group IIB 2a.
- N. sandiagensis* Fairchild 1977c: 158-60, pl. 1, fig. a-b. San Diego Trench, ca. 800 m. Group IIB 2a.
- N. seridentata* Hartmann-Schröder 1959: 138-42, fig. 100-10. Gulf of Fonesca, El Salvador. Group IIB 2c.
- N. succinea* (Leuckart 1847: 154-6, pl. 2, fig. 9, 11), as *Nereis succinea*. North Sea. Group IIB 2a. Includes *Neanthes perrieri* Saint-Joseph 1898: 288-92, pl. 14, fig. 69-77. See also Pettibone, 1963: 165-74, fig. 44a-e, fig. 45a-d; Day 1967: 321, fig. 14.9a-e; Imajima 1972: 108-10, fig. 32a-k, fig. 37; this study.
- N. trifasciata* (Ehlers 1901b: 106-7, pl. 12, fig. 1-7), as *Nereis trifasciata*. Juan Fernandez South America. Group IIB 1†.
- N. typhla* (Monro 1930: 105-6, fig. 36a, b), as *Nereis typhla*. Off South Georgia, 245 m. Group IIB 1.
- N. unifasciata* (Willey 1905: 271-2, pl. 4, fig. 85-8), as *Nereis unifasciata*. Gulf of Manaar, India. Group IIB 1. See also Fauvel, 1932: 93.
- N. uniseriata* Hutchings & Turvey 1982: 113-6, fig. 8a-c. South Australia. Group IIB 1†.
- N. vaalii* Kinberg 1866: 171. Southern Australia. Group IIB 1. Includes *Nereis albanyensis* Augener, 1913: 149-53, pl. 2, fig. 6u, textfig. 14a-c. See also this study.
- N. verrillii* (Grube 1878: 78-9, pl. 5, fig. 2), as *Nereis* (*Lycoris*) *verrillii*. Philippine Islands. Group IIB 2a.
- N. virens* (Sars 1835: 58)*, as *Nereis virens*. Norway. Group IIB 1†. See also Fauvel, 1923: 348-9, fig. 134g-k; Pettibone, 1963: 170-4, fig. 44f.
- N. vitabunda* (Pflugfelder 1933: 71-2, fig. 12a-d), as *Nereis vitabunda*. Sumatra. Group IIB 1.
- N. willeyi* (Day 1934: 39-40, fig. 6a-c), as *Nereis willeyi*. South Africa. Includes *Nereis* (*Neanthes*) *capensis* Willey 1904: 261, pl. 13, fig. 10, pl. 14, fig. 9-10 (Preoccupied). Group IIB 2a. See also Day, 1967: 320, fig. 14.8 l-p.

ENVIRONMENTAL INTERPRETATIONS OF LATE PLEISTOCENE OSTRACODE ASSEMBLAGES FROM THE RICHMOND RIVER VALLEY, NEW SOUTH WALES

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ABSTRACT: Ostracode assemblages from Evans Head and shallow bores in and near Lismore, N.S.W., are identified and counted. Five species and one subspecies are described as new, namely: *Cytherella loukornickeri*, *Cytherella lismorensis*, *Oculocytheropteron raybetei*, *Keijella jankeiji*, *Paradoxostoma evansheadensis* and *Tanella gracilis minor*.

Environmental interpretations based on these ostracode assemblages indicate two main facies types: one more exposed, open marine (Evans Head); the other representing the environments of a relatively protected bay with an immediate hinterland of generally low relief. Possibly, aquatic temperatures were rather warmer (up to 20°C) than at present in the region, when the sequences were deposited.

The assemblages offer conclusive proof that the sediments of the Gundurimba Clay, in which they occur, were deposited during a period when the embayment was entirely open to access of marine water, and that the Inner Barrier Beach ridges were deposited later. Models for emplacement of beach ridges must take account of this fact.

Pleistocene deposits in the Richmond River valley have been the focus of a number of investigations in recent years (Marshall & Thom 1976, Pickett 1981, Drury & Roman 1983), with the result that the Pleistocene and Recent sediments of this valley are becoming better known than those of most other valleys on the coast. This has been due in large part to a systematic hydrogeological study of the area undertaken by the N.S.W. Water Resources Commission. The stratigraphical results of this programme are summarised by Drury & Roman (1983) and Drury (in press).

The work of Marshall & Thom (1976) supplied the first reliable age determinations for any sediments associated with the Inner Barrier, and was thus of considerable significance in calibrating events in the evolutionary development of coastal landforms in northern N.S.W. Using a comparison with present-day distributions, Pickett (1981) was able to document a climatic shift for the period since 120 000 yr B.P. towards a cooler regime equivalent to a minimum of 2° of latitude, on the basis of an assemblage of scleractinian corals from the locality dated by Marshall & Thom (1976). Pickett (1981, p. 72) also anticipated an age for the widespread estuarine sediments of the valley upstream of Coraki similar to that of the coral locality described by him, although direct evidence was lacking at that time. The isotope ages of Drury & Roman (1983) have borne out this correlation, the ages from corals in particular (124 000 yr, 128 000 yr) occurring close to the range of determinations on corals from the Evans Head coral site (112 000 to 127 000 yr) (Marshall & Thom 1976).

LITHOSTRATIGRAPHY

In the Pleistocene succession of the Richmond River valley the most significant stratigraphic unit and the most widespread is the Gundurimba Clay (Drury &

Roman 1983), which occurs from Boatharbour, upstream of Lismore, and from a point 4 km east of Casino, eastwards beyond the present coastline (Drury & Roman 1983, fig. 3, Drury in press). Its base is everywhere unconformable. The unit rests on bedrock or on the South Casino Gravel in the area west of Coraki; to the east it overlies in addition either the Buckenoon Sand Member or the Doonbah Clay. In the west it is overlain by deltaic (?) sediments of the Greenridge Formation, in the central area by floodplain deposits and along the coast by the Woodburn Sand (the Inner Barrier). It is a dark, plastic clay, frequently containing marine invertebrates. The thickness varies greatly, reaching a maximum of 39.6 m in WRC 39140 (South Gundurimba), but only 8 m in WRC 39101 (Greenridge), 11 m in WRC 39135 (Boatharbour) and just 4.7 m in WRC 39152 (Evans Head). At the Evans Head coral locality it is only 2 m thick, though the top is eroded.

All the samples examined in the present article come from the Gundurimba Clay. The top of this unit lies at ca. +5 m AHD in WRC 39138 (Tuncester), ca. +4 m AHD in WRC 39140 (South Gundurimba), ca. -14 m in WRC 39149 (Tuckean Island) and -30 m in WRC 39152; hence the top of the unit lies at a progressively lower level towards the open ocean (data from Drury in press). Drury & Roman (1983) have indicated the contemporaneity of the coral locality and the Gundurimba Clay. We regard the coral locality as a shallow water deposit equivalent to the muds at deeper levels, as does Drury (pers. comm., Drury & Roman 1983, fig. 3). The coral-bearing strata (locality 18, Fig. 1) lie at approximately zero to -2 m AHD, and thus are considerably separated in depth (30 m) from the nearest known occurrence of true clays of the Gundurimba Clay (from -29.74 to -34.44 m in borehole WRC 39152, locality 10, Fig. 1), and are referred to the same formation. The

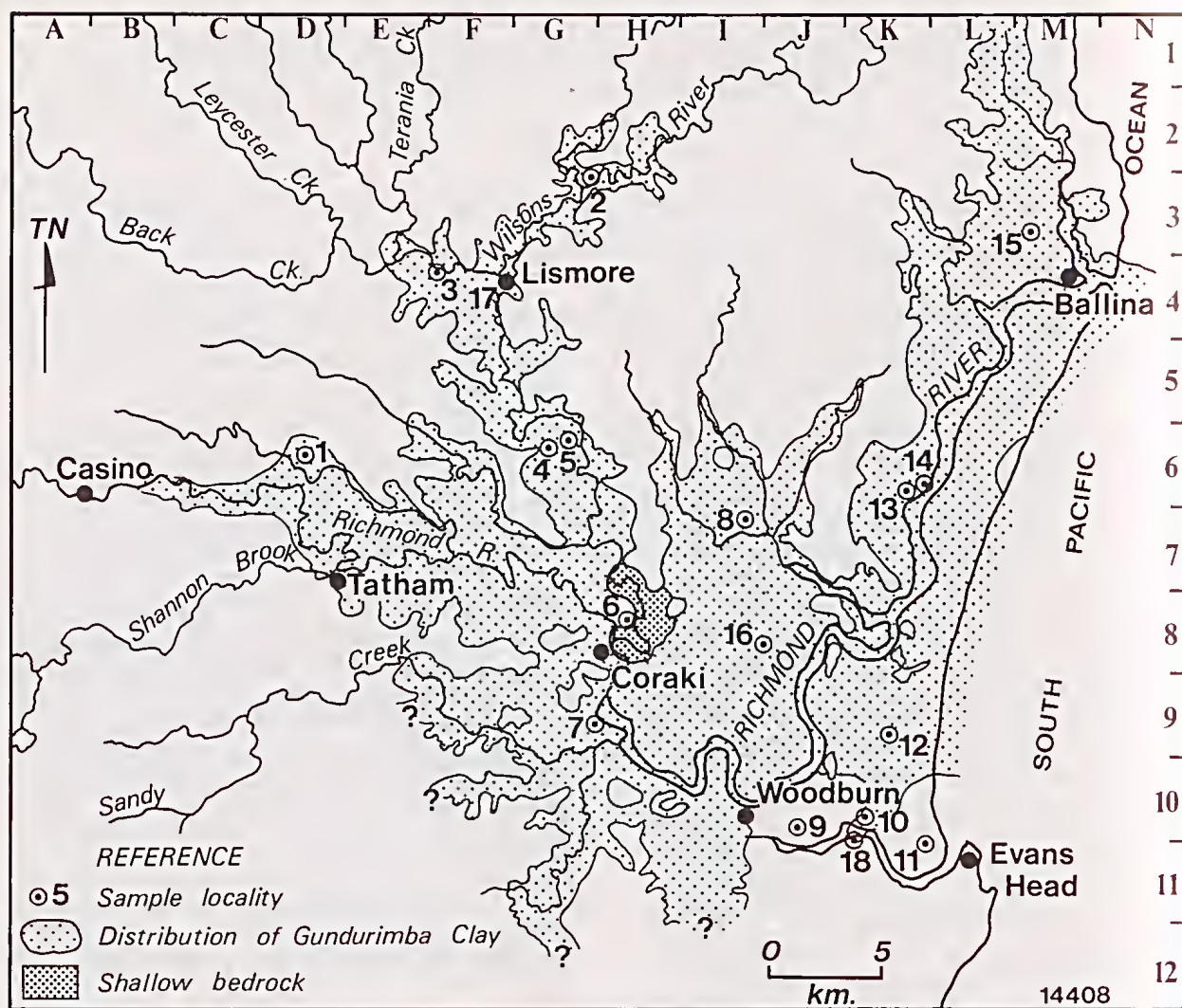


Fig. 1—Map of the lower Richmond River valley, showing location of samples discussed in the text and distribution of the Late Pleistocene Gundurimba Clay. Grid references to the numbered localities are given in brackets. 1, WRC 39101 Greenridge (D6). 2, WRC 39135 Boatharbour (G2/3). 3, WRC 39138 Tuncester (F4). 4, WRC 39139 South Gundurimba (G6). 5, WRC 39140 South Gundurimba (G6). 6, WRC 39143 Coraki (H8). 7, WRC 39145 Coraki (G9). 8, WRC 39149 Tuckean Island (I7). 9, WRC 39150 Woodburn (J10). 10, WRC 39152 Evans Head (K10). 11, WRC 39153 Evans Head (K10/11). 12, WRC 39155 North Evans Head (K9). 13, WRC 39157 Wardell (K6). 14, WRC 39158 Wardell (K6). 15, WRC 39163 Ballina (M3). 16, WRC 39165 Coraki East (I8). 17, Lismore Ambulance Station (F4). 18, Evans Head coral locality (J/K10/11).

shelly sediments of the coral bank include much mud, but this is locally diluted by sand presumably derived from the sandstones of the high bedrock adjacent to the locality, as well as by the great bulk of bioclastic material, resulting in a poorly sorted sediment. Particle size analysis of a sample from -1.5 m gave the following result: >2 mm, 26%; <2 mm >0.5 mm, 17%; <0.5 mm >0.25 mm, 15%; <0.25 mm >0.063 mm, 17%; <0.063 mm, 25%. The presence of such a proportion of fine-grained material we consider significant in relating the coral locality to the subsurface Gundurimba Clay.

The disparity in elevation of the top of the Gundurimba Clay between the coral locality and the nearest borehole reflects a sea floor topography falling 30 m in a distance of 1.5 km, by no means a remarkable drop. Fig. 3 of Drury & Roman (1983) and Fig. 1 herein show a southward prolongation of the Gundurimba Clay to include the coral site. In discussion Drury has also indicated that he considers the strata at the coral site a local variation in the Gundurimba Clay.

LOCATION OF SAMPLES

Ostracodes have been recovered from all localities

marked on Fig. 1. The locality most distant from the ocean, WRC 39135 Boatharbour, lies 106 km from the present mouth of the Richmond River, following the course of the River.

Fig. 1 indicates the distribution of the Gundurimba Clay, and thus roughly defines the shape of the embayment in which the formation was deposited. This embayment was restricted by two meridional basement highs, one approximately along grid-line G/H of Fig. 1, the other along lines J and K. Some points on these highs rise well above the level of the alluvial plain, and would have represented islands or reefs at the time of flooding of the embayment. The blank area at grid square L/M6 is not a high, but represents a point at which the Gundurimba Clay appears to have been eroded. Pickett (1981, p. 72) remarked, after an initial examination of microfossil assemblages from the samples reported on here, that planktonic foraminifera have not been recovered from samples further upstream than the more westerly of these highs.

The distribution of samples includes environments ranging from relatively open marine (10-15, 18), semi-restricted, between the basement highs (7, 8, 16) to points near the probable extremities of the embayment (1, 2) (see Fig. 1).

ECOLOGICAL RESULTS

Tables 1 and 2 indicate that by and large the Evans Head and Lismore district ostracode assemblages are markedly dissimilar, as appears from the following details:

1, *Cytherella lismorensis* sp. nov. does not occur at the Evans Head coral locality.

2, *Macrocyprina* sp. is not found in the WRC bores.

3, *Loxoconcha australis minor* subsp. nov. is the common loxoconchid at Evans Head but *L. tria* is far more common in the Lismore district WRC bores.

4, *Loxoconchella pulchra* does not occur in the WRC bores.

5, *Osticythere reticulata* is characteristic of the Lismore district bores, but also occurs at Wardell (in WRC 39157 it is associated with planktonic forams).

6, 'Neomonoceratina' *koenigswaldi* and *N. mediterranea* are absent from Evans Head.

7, *Oculocytheroan raybatei* sp. nov. does not occur in the WRC bores.

8, *Trachyleberis dampierensis* is represented by only one gerontic individual at Evans Head, although it occurs in two other bores outside the embayment.

9, *Paradoxostoma evansheadensis* sp. nov. is exclusive to Evans Head.

10, *Xestoleberis cedunaensis* is the characteristic xestoleberidid in the Lismore district bores, but *X. limbata* and *X. tigrina* characterise the Evans Head assemblages, *X. limbata* being the dominant Evans Head species.

Of the above taxa, note that *Macrocyprina* sp. occurs only as juvenile valves or as fragments of adult valves.

Clearly, the Evans Head assemblages (Table 1) and those from the WRC bores (Table 2) represent different biofacies, both nearshore. Of these two biofacies types, that at Evans Head is more open marine; whereas the Lismore district bore assemblages probably represent lagoonal, estuarine and protected bay facies. Fortunately, Hartmann (1979, 1980, 1981) has provided ecological notes for many taxa, and combining these with the senior author's experience allows relatively reliable ecological interpretations to be developed.

The most common species at Evans Head (Table 1) are: *Paranesidea* cf. *attenuata*, *Macrocyprina* sp., *Paracypris bradyi*, *Loxoconcha australis minor*, *Loxoconchella pulchra*, *Parakrithella australis*, *Callistocythere dorsotuberculata*, *C. keiji*, *Tanella gracilis*, *Oculocytheroan raybatei*, *Keijella jankeiji*, *Xestoleberis limbata* and *X. tigrina*. Of these, *C. dorsotuberculata* and *K. jankeiji* are also common in the WRC bores and can be ignored for comparative purposes.

Most of the Evans Head species are known phytal associates, often found among algae on rocks, or associated with seagrasses. This is particularly true for the dominant species *X. limbata*. The favoured substrates are sands, usually fine but including gravelly beach sands, and abrasion terraces (platforms). Depths would have been no greater than about 2-3 m. The assemblages are holomarine and more exposed than those from the WRC bores. The latter feature is indicated by the presence of juveniles and fragments of *Macrocyprina*, which is an offshore genus. Presumably, these specimens were washed inshore following storms. Further, *Oculocytheroan raybatei* indicates a sublittoral environment and probably also was washed into the assemblages rather than forming part of the bio-coenose. Important phytal indices include *Paranesidea* cf. *attenuata*, *Paracypris bradyi*, *Loxoconcha australis minor*, *Parakrithella australis*, *Paradoxostoma evansheadensis* and *Xestoleberis limbata*; the sand indices include *Loxoconchella pulchra* (sands with seagrass); *Xestoleberis tigrina* (sandy intertidals) and *Tanella gracilis* (a widely tolerant nearshore species with a preference for sandy substrates, including gravelly beaches).

Areally, as well as vertically, a greater number of facies is indicated by the WRC bore assemblages (Table 2, Appendix). The characteristic taxon is *Osticythere reticulata*; other common species are *Trachyleberis dampierensis* and *Keijella jankeiji*. Less common (occurring in 6 or fewer of the 15 bores) but important ecologically are the *Cytherella* species, *Phlyctenophora zealandica*, *Loxoconcha tria* and *Xestoleberis cedunaensis*.

Osticythere reticulata is an index for such marginal environments as estuaries and shoreline lagoons. The favoured substrates are shallow sands, silts and muds, especially when organic detritus is present.

The presence of *Osticythere reticulata* in the two boreholes at Wardell is not in agreement with both the fossil (Lismore district boreholes) and recent (Hawkesbury River) distributions, which indicate a clear association with an upper estuarine environment. The

TABLE 1
OSTRACODE SPECIES COUNTS FROM EVANS HEAD SAMPLES.

Species List	Sample Numbers—Evans Head																
	27	28	29	30	31	32	33	34									
Depth (m)	0.36	—	0.55	—	0.73	—	0.91	—	1.09	—	1.27	—	1.45	—	1.64	—	1.82
<i>Cytherella loukornickeri</i>	1	—	—	—	—	—	2	—	1	—	—	—	—	—	—	—	—
<i>Paranesidea</i> cf. <i>attenuata</i>	7	29	9	12	8	3	7	12	—	—	—	—	—	—	—	—	—
<i>Triebelina amicitiae</i>	2	—	1	—	—	1	1	—	—	—	—	—	—	—	—	—	—
<i>Macrocyprina</i> sp.	2	2	—	3	1	3	—	1	—	—	—	—	—	—	—	—	—
<i>Paracypris bradyi</i>	23	8	8	10	9	9	5	14	—	—	—	—	—	—	—	—	—
<i>Phlyctenophora zealandica</i>	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—	—	—
Indet. juv. Cypridacea	2	—	1	—	—	2	—	—	—	—	—	—	—	—	—	—	—
<i>Loxoconcha australis minor</i>	21	18	27	17	13	23	31	27	—	—	—	—	—	—	—	—	—
<i>Loxoconcha tria</i>	2	2	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
<i>Loxoconcha abditocostata</i>	1	—	1	—	—	—	—	2	—	—	—	—	—	—	—	—	—
<i>Loxoconchella pulchra</i>	—	1	1	—	1	1	3	—	—	—	—	—	—	—	—	—	—
<i>Hemicytheridea reticulata</i>	2	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—
<i>Bishopina vangoethemi</i>	2	—	1	—	2	—	1	—	—	—	—	—	—	—	—	—	—
<i>Parakrihellia australis</i>	7	12	11	9	9	15	5	9	—	—	—	—	—	—	—	—	—
<i>Callistocythere dorsotuberculata</i>	2	4	1	1	2	4	—	—	—	—	—	—	—	—	—	—	—
<i>Callistocythere keiji</i>	3	2	—	—	3	1	—	2	—	—	—	—	—	—	—	—	—
<i>Tanella gracilis</i>	3	1	—	1	2	2	—	—	—	—	—	—	—	—	—	—	—
<i>Oculocytheropteron raybatei</i>	4	—	1	—	1	—	1	6	—	—	—	—	—	—	—	—	—
<i>Ponticocythereis militaris</i>	—	1	1	—	1	—	1	—	—	—	—	—	—	—	—	—	—
<i>Trachyleberis dampierensis</i>	—	1*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Keijella jankeiji</i>	—	—	—	1	3	1	1	1	—	—	—	—	—	—	—	—	—
<i>Mutilus</i> sp.	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Paracytheroima sudaustralis</i>	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—
<i>Paradoxostoma evansheadensis</i>	1	3	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—
<i>Paradoxostoma</i> sp.	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
<i>Machaerina</i> sp.	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
<i>Xestoleberis cedunaensis</i>	1*	1	—	—	1	1	1	—	—	—	—	—	—	—	—	—	—
<i>Xestoleberis limbata</i>	106	113	135	149	133	124	133	115	—	—	—	—	—	—	—	—	—
<i>Xestoleberis tigrina</i>	8	3	3	4	9	14	10	9	—	—	—	—	—	—	—	—	—
TOTAL	200	201	202	209	201	207	204	201	—	—	—	—	—	—	—	—	—

Note that Samples 25 and 26 were barren of Ostracoda. These represent the topmost 36 cm of sediment.

* Indicates a gerontic specimen.

geographical situation (see Fig. 1) suggests that this is unlikely at Wardell. Both ostracode and foraminiferal assemblages are very poor in species, and *O. reticulata* is represented by only two specimens from WRC 39157 and six specimens from WRC 39158. The situation is rendered even less clear by the presence of a single globigerinid in WRC 39157. It seems most likely that these apparently mixed assemblages are due to some local complication, the details of which are not clear from the available data. It may be that these localities represent a shoreline lagoon rather than part of an estuarine system.

Of the other species, '*N.*' *koenigswaldi* and *X. cedunaensis* are associated with sandy to muddy substrates and also with mangroves. The *Cytherella* species and *P. zealandica* on the other hand indicate a shallow water phytobenthos.

Among the rarer species, *Aspidoconcha* sp. represents a genus which is commensal on burrowing

isopods and amphipods, and *Neomonoceratina mediterranea* is associated with sandy beaches as is *Pseudopsammocythere* sp. Further, *Paracytheroma sudaustralis* is a known associate of marginal environments (McKenzie 1978, Hartmann 1980) usually indicating nearby freshwater influences.

In summary, the WRC bore assemblages at Coraki and upstream indicate a variety of marginal facies such as could be expected in a relatively protected bay, with an immediate hinterland of low relief including meandering estuaries and nearshore lagoons; but also with associated fine sand beaches and silty littorals having an interstitial and burrowing (endobenthic) fauna. Mangroves were certainly present. The lower intertidal and subtidal parts of such beaches were colonised by seagrasses.

A number of species indicate a warmer temperature regime for the assemblages than is typical of the region today. These species include *Paranesidea* cf. *attenuata*,

Triebelina amicitiae, *Bishopina vangoethemi*, *Hemicytheridea reticulata* and *Keijella jankeiji*; all belong in genera which are more typical of tropical and sub-tropical assemblages. The mean summer shallow water temperature limit for the faunas may have been about 20°C. Hartmann (1980, p. 139) indicated that at this temperature *Loxoconcha trita* begins to cut out, unlike *L. australis minor*, which can tolerate higher temperatures.

The Appendix, which gives the vertical distributions of the WRC bore assemblages, indicates that this suite of marginal and relatively protected facies shifted with time. The available samples are too few for an analysis of their variation. In general, however, the more marine facies are represented by bores 39139, 39140, (South Gundurimba), 39143, 39145 (Coraki), 39149 (Tuckean Island), 39152 (Evans Head) and, possibly, 39155

(North Evans Head), while more estuarine and lagoonal conditions are represented by bores 39101 (Greenridge), 39135 (Boatharbour), 39138 (Tuncester), 39157 and 39158 (Wardell). Bores 39163 (Ballina) and 39165 (Coraki East) cannot be interpreted ecologically with much confidence. The Lismore Ambulance Station Bore could be dominantly estuarine, but, unfortunately, only one assemblage from this bore has a known depth.

Sufficient ostracodes were picked from bores WRC 39135 (Boatharbour), 39140 (South Gundurimba), 39145 (Coraki) and from Evans Head to allow definition of the estuarine horizons *vis à vis* their holomarine counterparts and to provide for a more detailed interpretation of the former group.

In general, the estuarine horizons are characterised by assemblages dominated by the species *Osticythere reticulata*, *Trachyleberis dampierensis* and *Keijella*

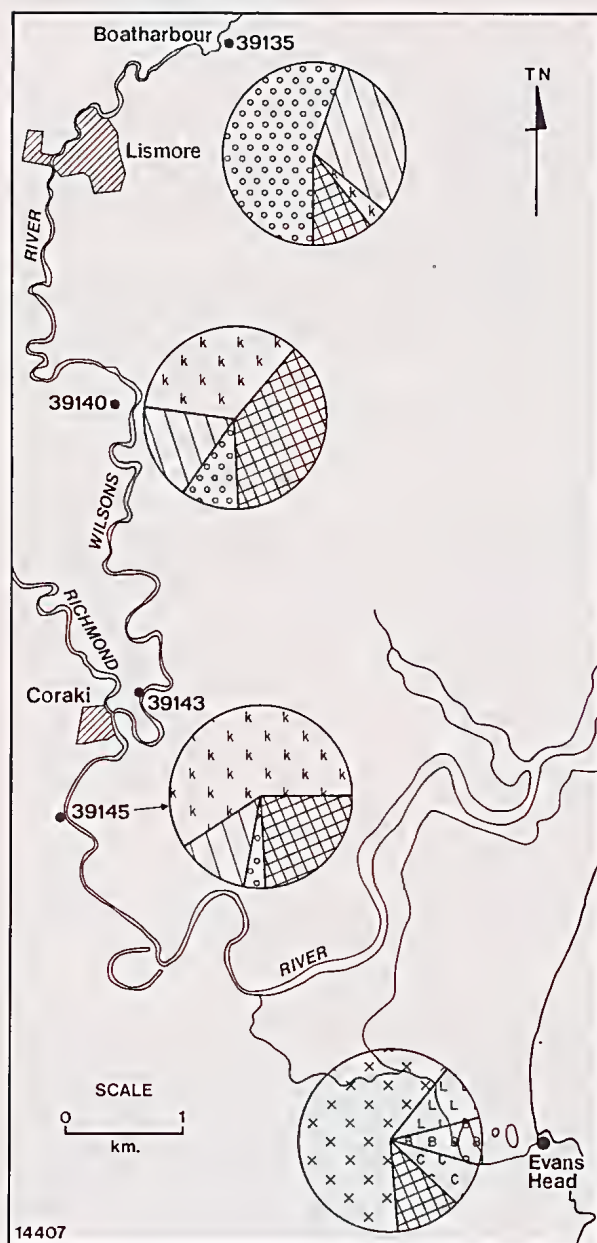
TABLE 2
OSTRACODE SPECIES FROM WRC BORES NEAR LISMORE, N.S.W.

Locality/WRC bore no.	39101	39135	39138	Ambulance Station	39139	39140	39143	39145	39149	39165	39152	39155	39157	39158	39163
<i>Cytherella loukornickeri</i>	—	—	—	—	X	1	—	X	X	—	X	X	—	—	—
<i>Cytherella lismorensis</i>	—	—	—	—	X	4	—	X	X	—	—	—	—	—	—
<i>Paranesidea cf. attenuata</i>	—	—	—	—	X	7	X	—	—	—	—	—	—	—	—
<i>Paracypris bradyi</i>	—	—	—	—	X	2	X	—	—	—	—	—	—	—	—
<i>Phlyctenophora zealandica</i>	—	X	—	X	—	2	—	X	X	—	—	—	—	—	—
<i>Propontocypris</i> sp.	—	—	X	—	—	X	—	—	—	—	—	—	—	—	—
<i>Loxoconcha australis minor</i>	—	—	—	—	X	3	—	X	—	—	X	—	—	—	—
<i>Loxoconcha trita</i>	—	—	X	X	X	34	—	X	X	—	—	—	—	—	—
<i>Hemicytheridea reticulata</i>	—	—	—	—	X	—	—	—	X	—	—	—	—	X	—
<i>Cytherurid?</i> sp. juv.	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
<i>Bishopina vangoethemi</i>	—	—	—	—	X	—	X	X	—	—	—	—	—	—	—
<i>Osticythere reticulata</i>	X	X	X	X	X	17	—	X	—	—	—	—	X	X	—
<i>'Neomonoceratina' koenigswaldi</i>	X	—	X	X	—	15	—	X	—	—	—	—	—	X	—
<i>Neomonoceratina mediterranea</i>	—	—	—	—	X	2	—	—	—	—	—	—	—	—	—
<i>Parakrithella australis</i>	—	—	—	—	—	4	—	—	X	—	—	—	—	—	—
<i>Callistocythere dorsotuberculata</i>	—	X	—	—	X	1	X	X	—	X	X	—	—	—	—
<i>Callistocythere hartmanni</i>	X	—	—	X	—	—	—	—	—	—	—	—	—	—	—
<i>Callistocythere keiji</i>	—	—	—	—	X	1	X	—	—	—	—	—	—	—	—
<i>Tanella gracilis</i>	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—
<i>Tanella gracilis minor</i>	—	—	—	X	—	—	—	—	—	—	—	—	—	—	—
<i>'Pectocythere' portjacksonensis</i>	—	—	X	—	X	—	—	—	—	—	—	—	—	—	—
<i>Pontocythereis militaris</i>	—	—	—	—	—	—	X	—	—	—	—	—	—	—	—
<i>Trachyleberis dampierensis</i>	—	X	X	—	X	34	X	X	X	X	X	X	—	—	—
<i>Australinnoosella</i> sp.	—	—	—	—	—	—	—	—	—	—	X	—	—	—	—
<i>Cleioocythereis rastromarginata</i>	—	—	—	—	X	3	—	—	—	—	—	—	—	—	—
<i>Bradleya</i> juv. indet.	—	—	—	—	—	—	—	—	X	—	—	—	—	—	—
<i>Keijella jankeiji</i>	X	X	X	X	X	62	—	X	X	X	X	—	—	—	X
<i>Paracytheroma sudaustralis</i>	—	—	—	X	—	1	—	—	—	—	X	—	—	—	—
<i>Machaerina</i> sp.	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
<i>Xestoleberis cedunaensis</i>	X	—	—	—	X	16	—	X	X	—	—	—	—	—	—
<i>Xestoleberis limbata</i>	—	—	X	—	X	—	—	—	—	—	—	—	—	—	—
<i>Xestoleberis</i> sp.	—	—	—	—	—	—	—	X	—	—	—	—	—	—	—
<i>Aspidoconcha</i> sp.	—	—	—	—	—	—	—	—	—	—	X	—	—	—	—
<i>Pseudopsammocythere</i> sp.	—	—	—	—	—	—	—	X	—	—	—	—	—	—	—

The count was made at the 20-21 m sample in Bore No. 39140. X = present; — = absent.

The localities are arranged according to their distance from the ocean, the most distant at the left.

jankeiji. These three species, for example, form 92% of the ostracode assemblage at Boatharbour, a well-defined estuarine bore, but less than 1% of the species at the holomarine Evans Head site.



- o = *Osticythere* L = loxoconchids
 k = *Keijella* B = Bairdiaceo
 // = *Trachyleberis* c = Cypridaceo
 x = xestoleberidids [cross-hatching] = others

Ostracoda
 Foraminifero : 39135 = 0.66; 39145 = 0.45

Of the three species, *Osticythere reticulata* (56%) is dominant in the estuarine environments which lie furthest upstream); in these environments *Keijella jankeiji* is rare (3%) and *Trachyleberis dampierensis* (33%) is very common (WRC 39135, Fig. 2). Downstream from Boatharbour *O. reticulata* (8%) begins to cut out and the assemblage is dominated by *K. jankeiji* (29%) and *T. dampierensis* (16%)— this is the situation in WRC bore 39140 (Fig. 2). Finally, near the mouth of the former estuary, *O. reticulata* (3%) is rare, and the assemblage is dominated by *K. jankeiji* (55%), with *T. dampierensis* (11%) less common (WRC 39145, Fig. 2). Confirmation of the interpretation that WRC 39145 is located in the channel of a former estuary is provided by the nearby WRC bore 39143, which is dominated by polyhaline (lagoonal) species (Fig. 2). It seems that the three species discussed above can be considered indices for an ecological gradient from well-defined estuarine to near marine environments. This is probably the most useful result to emerge from our study of the ostracode faunas in the Evans Head and Lismore district bores. The ostracode faunas show a clear discontinuity between the two seaward localities of Fig. 2, which is correlated with the change from estuarine to marine conditions.

IMPLICATIONS OF THE STUDY

The ecological results clearly support the statement of Pickett (1981, p. 72) that the "estuary was wide open at some stage prior to barrier formation", i.e. at the time of deposition of the Gundurimba Clay.

It is helpful to draw an analogy between the Richmond River valley during Gundurimba time and a modern embayment, such as that of the Hawkesbury River (Broken Bay), on which rather more data are available than for most others. The more seaward of the basement highs would come closest to representing the entrance to Broken Bay, the width of the entrance being approximately 11 km, though broken by a series of islands with a maximum separation of approximately 3 km. The entrance to Broken Bay has an unbroken width of 4 km, the single island, Lion Island, being set well back, and serving more to divide the two major arms of the embayment than to obstruct general access of ocean water. The two estuaries may then be con-

Fig. 2—Proportional representation of ostracode taxa in samples from a range of locations. The genera *Osticythere*, *Keijella* and *Trachyleberis*, typical of estuarine conditions, together comprise more than 60% of the three assemblages from the more inland area, but less than 1% of the fauna from near Evans Head, which is dominated by holomarine xestoleberidids, indicating clearly that the Evans Head locality is not estuarine. Within the three estuarine faunas, *Keijella*, characteristic of the outer estuary, is progressively less significant upstream, whereas *Osticythere*, typical of the inner estuary, shows the reverse distribution. Ostracode/foraminifera ratios are 0.66 for WRC 39135, 0.45 for WRC 39145. Key to hachures: o = *Osticythere*; *Keijella*; X = xestoleberidids; L = loxoconchids; B = Bairdiacea; C = Cypridacea; diagonal lines = *Trachyleberis*; cross-hatching = other groups.

TABLE 3
MICROFAUNAL ASSEMBLAGES AND ASSOCIATED ENVIRONMENTAL FACTORS, HAWKESBURY RIVER.

Sample numbers	1	2	3	4	5	6	7	8	9	10	11	12
OSTRACODA												
<i>Paracypria</i> sp.							1					
<i>Osticythere reticulata</i>	2	1		4		2	27	125	186	22	14	27
<i>Callistocythere</i> sp.									1	3		
' <i>Hiltermannicythere</i> ' <i>bassiounii</i>												
<i>reticulata</i>								1	5			
trachyleberidinid sp.									1			
' <i>Bythocythere</i> ' sp.								1				
FORAMINIFERA												
<i>Protoschista findens</i>									1			
<i>Miliammina fusca</i>											2	
<i>Haplophragmoides australiensis</i>						5			1			2
<i>Haplophragmoides canariensis</i>									2			11
<i>Ammonobaculites foliaceus</i>							1		16	3		
<i>Trochammina inflata</i>	1					2			3	1		5
<i>Quinqueloculina seminula</i>								1		1		
<i>Triloculina oblonga</i>								5				
<i>Spirillina vivipara</i>							1					
<i>Discorbis mirus</i>		1										
<i>Ammonia beccarii</i>							1		37	5		
<i>Elphidium advenum</i>									1			
<i>Cribronion hawkesburiensis</i>									2			
Molluscs						X		X	X	X	X	X
Bryozoans								X	X			
Serpulids											X	
Plant remains						X	X	X	X	X		
framboidal pyrite												X
> silt fraction (%)	5.2	14.4	91.4	3.6	90.6	4.0	0.6	0.4	4.6	3.4	7.0	1.0
depth (m)	0.2	2.5	5.7	15.0	17.5	0.25	2.5	10.0	14.5	20.0	3.0	2.0
distance from bank (m)	b	20.0	40.0	*	25.0	p	25.0	50.0	*	50.0	*	2.0

1-5, Gunderman, GR 40848666. 6-10, Gentlemans Reach, GR 41658640. 11-12, Road bridge, Mangrove Creek, GR 41568706. All map references (yards) refer to Sydney 1:250,000 sheet. 1-5 were collected at low tide; 6-10 were collected when tide was about 0.6 m below HWM. Of the total of 12 samples, 3 and 5 were barren. Determinations by K.G.M.

* = mid channel; b = bank between mangrove roots; p = limit of mangrove pneumatophores; X = present.

sidered roughly comparable at this point, the greater number of smaller gaps in the Richmond embayment compensating for the greater width of the Hawkesbury entrance.

On this basis, the extreme samples from the Richmond embayment (Greenridge and Boatharbour) would have lain 27 km and 35 km respectively from the entrance, thus corresponding to points such as Spencer at the junction of Mangrove Creek with the Hawkesbury, and either Gunderman on the main river or Lower Mangrove on Mangrove Creek.

Table 3 records the results of a recent survey by us of Hawkesbury River sites (Gunderman; Gentlemans Reach near Spencer; Mangrove Creek). It includes the ostracodes and foraminiferans as well as some associated faunal elements and other environmental factors (depth, distance from bank, percentage coarser than silt size in the substrate). As at Boatharbour in the Richmond embayment assemblages, *Osticythere*

reticulata clearly predominates at the Hawkesbury River sites, thus vindicating the analogy we have drawn above. The Gunderman samples more closely resemble those from Greenridge than those from Boatharbour, which is in accord with the positions of those localities on the main river channels.

The presence of a contemporaneous subaerial sand barrier in the present position of the Inner Barrier would have produced such a restriction in circulation that estuarine faunas as varied as that at Boatharbour (7 species) could not have survived. This, coupled with the straightforward marine nature of the assemblage at the Evans Head coral locality (inside the Inner Barrier), makes it obvious that the Inner Barrier must have been emplaced well after the rise in sea level which flooded the estuary. It is generally held (following Thom 1965) that the Inner Barrier ridges were established during a time when the sea level was higher than at present. Roy & Thom (1981, p. 483) produced a model for barrier

emplacement by which "during each transgression, mud . . . accumulated in an estuary behind a landward-moving barrier that was mostly reworked and incorporated into a new barrier . . ."; in other words, an emergent barrier was constantly present between ocean and estuary. On the present evidence, as well as that presented elsewhere on the basis of planktonic foraminifera (Pickett 1983), this model is untenable. Therefore, emplacement of the Inner Barrier beach ridges must have taken place either near the still stand of maximum sea level, or during the early stages of regression, or conceivably at a later high stand of sea level (Pickett *et al.* in press). Whenever it occurred, the establishment of the barrier would rapidly have terminated estuarine sedimentation of the type implied by the faunas of the Gundurimba Clay.

No analogy is known on today's coastline of a situation which is sheltered enough to allow muddy sediment to accumulate, but at the same time open enough for marine circulation adequate to allow ostracode, coral and planktonic foraminiferan assemblages characteristic of open situations to occur. This anomaly, first pointed out by Pickett (1983), is apparent also in the style of coral assemblages at Evans Head (Pickett 1981) and North Stradbroke Island (Pickett *et al.* in press), both of which imply better access of oceanic water than in modern Moreton Bay.

Two circumstances suggest that the emplacement is associated with the peak of the interglacial, though the evidence is somewhat equivocal.

Firstly, the repetition of a considerable number of similar ridges making up the barrier system clearly implies recurrent events of similar type, possibly with considerable intervals between them. The relatively constant height of the ridges implies that there was little change in sea level during emplacement, suggesting that the ridges were not formed during a regressive period.

Secondly, the Gundurimba Clay is overlain along its seaward margin by the Woodburn Sand (the Inner Barrier), which terminated deposition of the earlier formation. Elsewhere it is overlain by very thin floodplain deposits or by the Greenridge Formation in the most landward parts. This latter is regarded as deltaic by Drury (in press); if this is so it may represent sediments

laid down in the now relatively fresh waters of the embayment largely dammed by the youthful Inner Barrier.

A corollary of this provides an estimate of maximum sea level. The top of the Gundurimba Clay in WRC 39138 (Tuncester) is ca. +6 m AHD. It is overlain by ca. 6 m of deltaic Greenridge Formation and ca. 1 m of floodplain deposit. If the Greenridge Formation was indeed deposited under water, the top water level may thus have been as high as +12 m AHD. This is however considerably higher than the highest point on the Inner Barrier ridge system (ca. 8 m), so there is some inconsistency.

TAXONOMIC NOTES

Recent work by Hartmann (1979, 1980, 1981) and McKenzie (1967, 1978) has complemented the early work of Brady (1866, 1880)—based on material sent to him by private collectors and that from several conveniently sited "Challenger" stations—so that the marine ostracode fauna of southeastern Australia is becoming relatively well known. The following notes indicate recognition of some remaining taxonomic uncertainties with this Pleistocene-Holocene N.S.W. fauna; both are at the generic level.

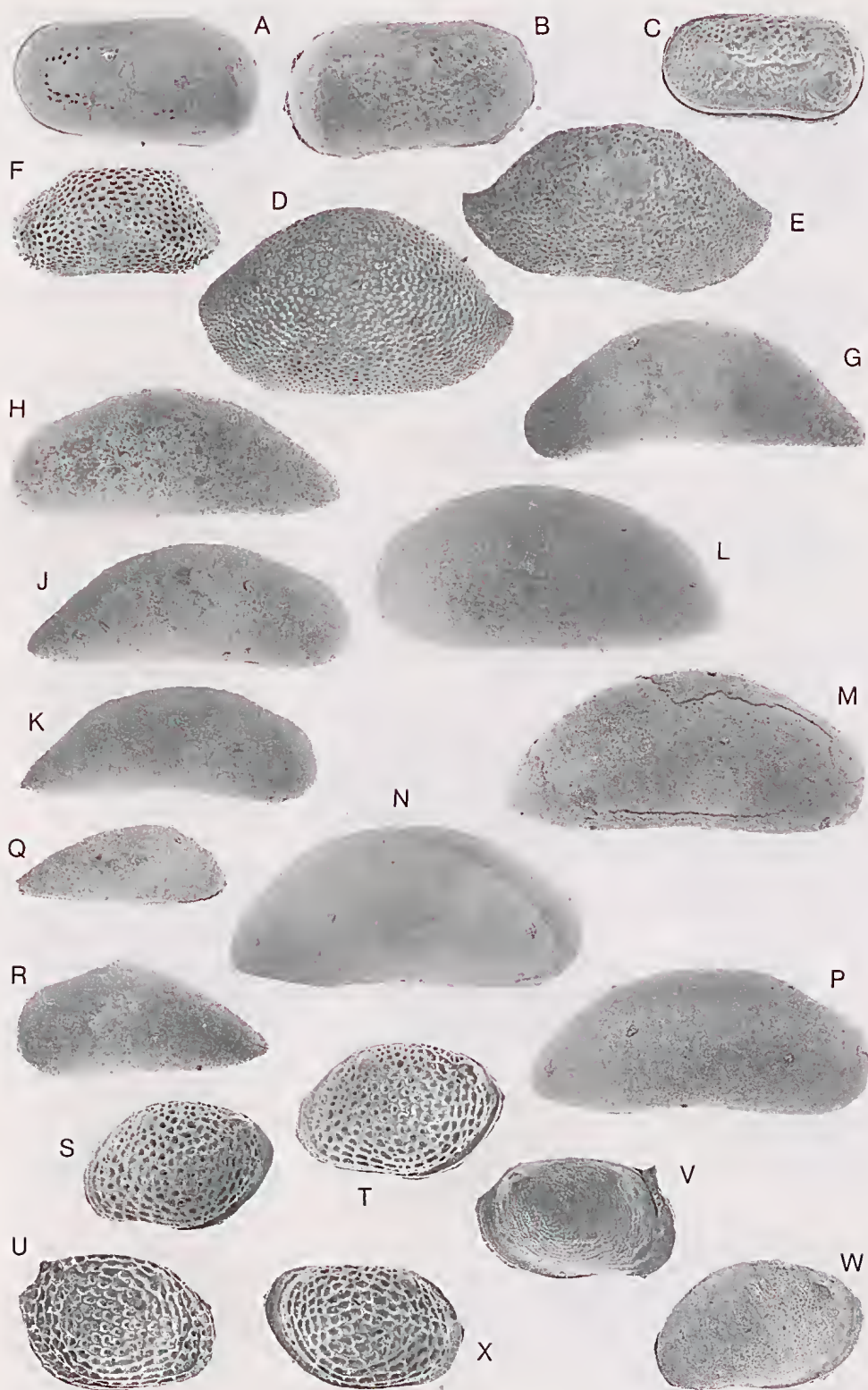
'*Neomonoceratina*' *koenigswaldi* Keij 1954.

McKenzie & Sudijono (1981) drew attention to the need for a revision at the generic level of this commonly encountered Indo-West Pacific species. What is needed is a comparison of living material of this species with another, more typical, living *Neomonoceratina* (such as *mediterranea* Ruggieri 1953) in order to decide whether or not there is soft parts evidence to complement the gross size difference between *koenigswaldi* and all other *Neomonoceratina* species in order to validate a new generic name.

'*Pectocythere*' *portjacksonensis* (McKenzie 1967).

There is a general agreement among interested workers (correspondence and verbal discussions with Hartmann and Bentley) that this species represents a new generic taxon; a manuscript name for the genus already exists in a Macquarie University thesis which, it is hoped will soon be submitted for publication.

Fig. 3—Representative ostracodes from the Late Pleistocene Gundurimba Clay. Locality numbers refer to Fig. 1. All $\times 50$. A, B, *Cytherella loukornickeri* sp. nov., loc. 18, 0.97–1.09 m. A, holotype \varnothing LV, MMMC01646. B, paratype \varnothing RV, MMMC01647. C, *Cytherella lismorensis* sp. nov., holotype σ carapace, loc. 4, 13–14 m, MMMC01648. D, E, *Paranesidea attenuata* (Brady), loc. 18, 0.36–0.55 m. D, \varnothing LV, MMMC01649. E, \varnothing RV, MMMC01650. F, *Triebelina amicitiae* Keij, \varnothing LV, loc. 18, 0.36–0.55 m, MMMC01651. G, *Macrocyprina* sp., juvenile LV, loc. 18, 0.55–0.73 m, MMMC01652. H–K, *Paracypris bradyi* McKenzie. H, \varnothing LV, loc. 18, 0.91–1.09 m, MMMC01655. J, \varnothing RV, loc. 18, 0.36–0.55 m, MMMC01654. K, σ RV, same, MMMC01653. L–P, *Phlyctenophora zealandica* Brady. L, \varnothing LV, loc. 8, 19–20 m, MMMC01659. M, \varnothing RV, loc. 18, 1.64–1.82 m, MMMC01657. N, \varnothing RV, loc. 18, 1.45–1.64 m, MMMC01656. P, σ RV, loc. 8, 19–20 m, MMMC01658. Q, R, *Propontocypris* sp. juv., loc. 5, 21–22 m. Q, RV, MMMC01661. R, LV, MMMC01660. S–U, *Loxoconcha australis minor* Hartmann. S, \varnothing LV, loc. 18, 0.36–0.55 m, MMMC01662. T, \varnothing LV, loc. 18, 1.45–1.64 m, MMMC01663. U, \varnothing RV, same, MMMC01664. V, W, *Loxoconcha abditocostata* Hartmann, loc. 18, 0.36–0.55 m. V, \varnothing RV, MMMC01665. W, \varnothing LV, MMMC01666. X, *Loxoconcha trita* McKenzie, \varnothing RV, loc. 18, 0.36–0.55 m, MMMC01667.



The species *portjacksonensis* has a similar size and general shape to *Tanella gracilis minor* which is described in this paper. More careful examination, however, indicates differences in the surface ornament and in the internal marginal features (especially the radial pore canals) as well as in the hinge—the *portjacksonensis* hinge is a pentodont type—which enables the two taxa to be separated readily.

SYSTEMATICS

Family CYTHERELLIDAE Sars 1866

Genus *Cytherella* Jones 1849

Cytherella loukornickeri McKenzie sp. nov.

Figs 3A, B, 6A, B

ETYMOLOGY: For Dr L. S. Kornicker, Smithsonian Institution.

DESCRIPTION: Carapace medium sized; elongate subrectangular in lateral view; anterior broadly rounded; posterior also broadly rounded, especially in females where it is swollen to accommodate the internal brood chamber; dorsum and venter both nearly straight; surface lustrous, smooth except for a discontinuous girdle of pits anteromedially, with a slight depression in the adductor muscle scar region; greatest height medial in males, posteromedial in females. In dorsal view subcuneate; tapering anteriorly, broader posteriorly. Internally: pseudoradial pore canals well developed anteriorly; normal pore canals simple, unrimmed; adductor muscle scars biserial, pinnate; hinge simple, adont, right valve (RV) accommodates left (LV) and is somewhat larger in consequence. Sex dimorphism distinct—females swollen and males slender posteriorly. Soft parts unknown.

DIMENSIONS: Holotype ♀ LV MMMC01646, length 0.69 mm, height 0.31 mm.

TYPE LOCALITY: Evans Head coral locality, N.S.W. (locality 18, Fig. 1) at 0.91–1.09 m.

OTHER LOCALITIES: The species also occurs in samples from 0.36–0.55 m and 1.09–1.27 m at locality 18, and in WRC bores 39139, 39140, 39145, 39149, 39152, 39155 (cf. Appendix).

REMARKS: The species resembles most closely *Cytherella pulchra* Brady 1866, but differs in that the surface is not completely smooth but bears a discontinuous girdle of pits anteromedially.

Cytherella lismorensis McKenzie sp. nov.

Figs 3C, 6C

ETYMOLOGY: For Lismore, N.S.W.

DESCRIPTION: Carapace medium sized; subrectangular in lateral view; anterior broadly rounded; posterior broadly subtruncate, swollen in females to accommodate the internal brood chamber; dorsum and venter both nearly straight; surface pitted by numerous shallow pits, in females smooth over part of the swollen posterior, slightly depressed in the adductor muscle scar region; greatest height posteromedial in females. In dorsal view compressed, subcuneate; tapering anteriorly, broader posteriorly. Internally: pseudoradial pore canals present; duplicature marginal; normal pore canals simple, unrimmed; adductor muscle scars biserial, pinnate; hinge adont; RV and LV subequal. Sex dimorphism distinct—females swollen and males slender posteriorly. Soft parts unknown.

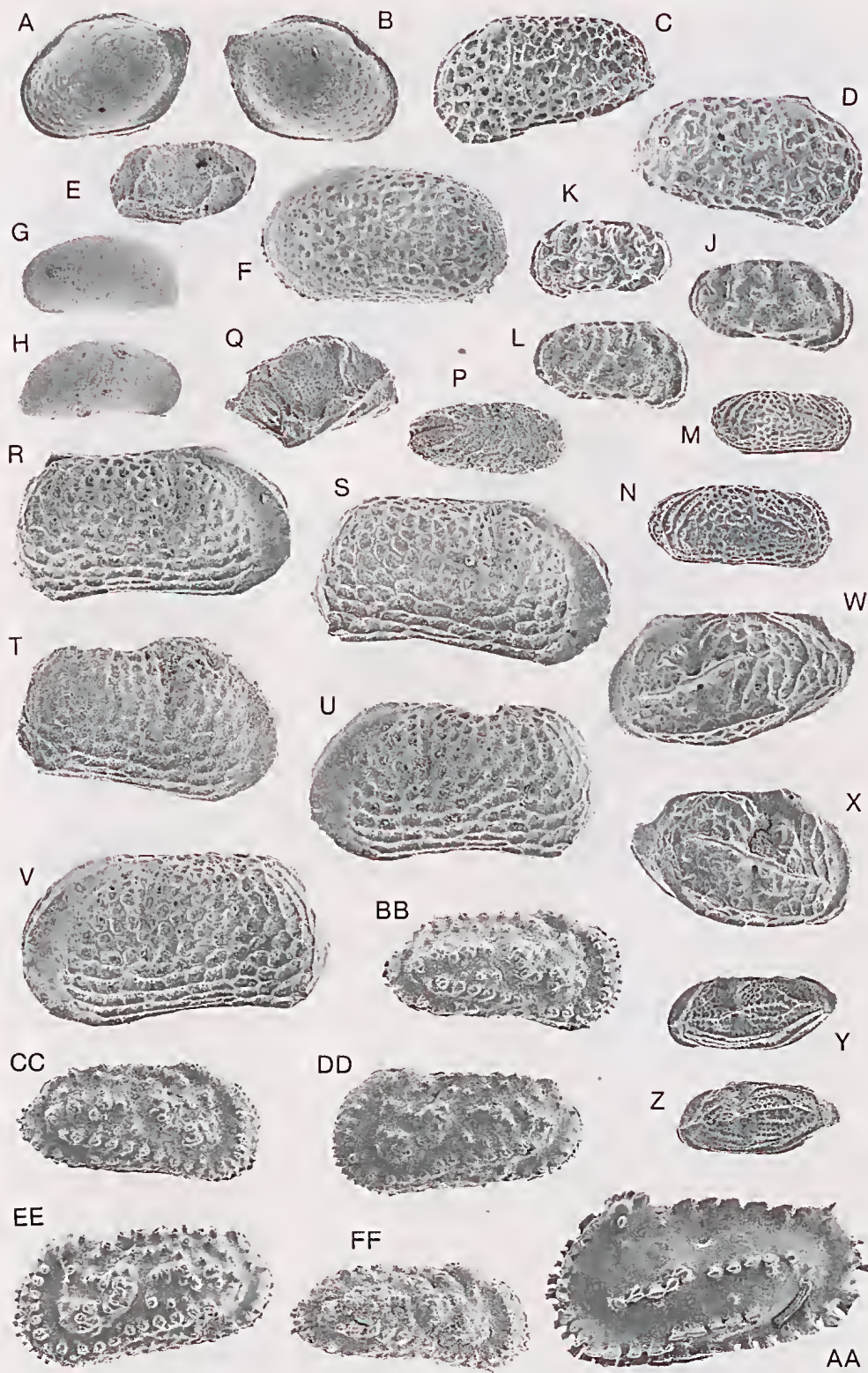
DIMENSIONS: Holotype ♂ carapace MMMC01648, length 0.56 mm, height 0.33 mm, breadth 0.25 mm.

TYPE LOCALITY: WRC bore 39139, South Gundurimba, near Lismore, N.S.W., 13–14 m.

OTHER LOCALITIES: The species also occurs in bores 39140, 39145, 39149 (cf. Appendix).

REMARKS: This species bears little resemblance to any previously described Australian cytherellid. It is closest to the Indo-Malaysian species *Cytherella semitalis* Brady, 1868, but has a different pattern of pits and lacks the clear medial area in each valve which characterises that species. The pits in *C. semitalis* are much larger

Fig. 4—Representative ostracodes from the Late Pleistocene Gundurimba Clay. Locality numbers refer to Fig. 1. All $\times 50$. A, B, *Loxoconchella pulchra* McKenzie, loc. 18, 0.55–0.73 m. A, ♀ LV, MMMC01668. B, ♀ RV, MMMC01669. C, D, *Hemicytheridea reticulata* Kingma, loc. 4, 13–14 m. C, ♀ LV, MMMC01670. D, ♀ RV, MMMC01671. E, cytherid? sp. juv., LV, loc. 5, 20–21 m, MMMC01672. F, *Bishopina vangoethemi* Wouters, ♀ LV, loc. 18, 0.36–0.55 m, MMMC01673. G, H, *Parakrithella australis* McKenzic, loc. 18, 0.36–0.55 m. G, ♀ LV, MMMC01674. H, ♀ RV, MMMC01675. J, *Callistocythere dorsotuberculata* Hartmann, ♀ RV, loc. 18, 0.36–0.55 m, MMMC01676. K, L, *Callistocythere* cf. *keiji* (Hartmann). K, ♂ LV, loc. 5, 20–21 m, MMMC01678. L, ♂ RV, loc. 7, 17–18 m, MMMC01677. M, *Tanella gracilis minor* subsp. nov., holotype ♀ RV, loc. 17, 14–15.5 m, MMMC01683. N, *Tanella gracilis gracilis* Kingma, ♀ RV, loc. 18, 0.36–0.55 m, MMMC01679. P, "*Pectocythere*" *portjacksonensis* (McKenzie), carapace, dorsal view, loc. 3, 20–21 m, MMMC01684. Q, *Oculocytheropteron raybatei* sp. nov., holotype ♀ RV, loc. 18, 0.36–0.55 m, MMMC01686. R–V, *Osticythere reticulata* Hartmann. R, ♀ RV, loc. 2, 20–21 m, MMMC01688. S, ♂ RV, loc. 5, 20–21 m, MMMC01690. T, ♀ RV, loc. 2, 20–21 m, MMMC01687. U, ♂ LV, same, MMMC01689. V, ♂ LV, loc. 5, 20–21 m, MMMC01691. W, X, "*Neononoceratina*" *koenigswaldi* Keij, loc. 5, 20–21 m. W, ♂ LV, MMMC01693. X, ♀ RV, MMMC01692. Y, Z, *Neononoceratina mediterranea* Ruggieri, loc. 5, 20–21 m. Y, ♂ LV, MMMC01694. Z, ♀ LV, MMMC01695. AA, *Ponticythereis militaris* (Brady), ♀ LV, loc. 18, 0.73–0.91 m, MMMC01696. BB–FF, *Trachyleberis dampierensis* (Hartmann). BB, ♂ RV, loc. 5, 20–21 m, MMMC01701. CC, ♂ RV, same, MMMC01700. DD, ♀ LV, loc. 2, 20–21 m, MMMC01698. EE, ♀ LV, loc. 18, 0.55–0.73 m, MMMC01697. FF, ♂ RV, loc. 2, 20–21 m, MMMC01699.



than in *C. lismorensis* and the shape more elongate; its size is 0.61 mm (examination of Brady's 'Fonds de la Mer' types in the Brady Collection at the Hancock Museum, Newcastle-upon-Tyne, Reg. No. B57).

Family LEPTOCYThERIDAE Hanai 1957

Genus *Tanella* Kingma 1948

Tanella gracilis Kingma, 1948 *minor* McKenzie
subsp. nov.

Figs 4M, 6J-L

ETYMOLOGY: *minor* (L.) = lesser, smaller.

DESCRIPTION: This subspecies has all the characteristics of the nominate taxon but is consistently more fragile and smaller in adult moults.

DIMENSIONS: Holotype ♀ RV MMC01683, length 0.39 mm, height 0.19 mm. Paratype ♂ RV MMC01682, length 0.38 mm, height 0.18 mm.

TYPE LOCALITY: Ambulance Station bore, 14-15.5 m, Lismore, N.S.W.

REMARKS: *Tanella gracilis* was first recorded from the coast of N.S.W. by Hartmann (1981); and it is common in the Evans Head samples, where its size is about 0.51 mm—considerably greater than that of the new subspecies.

The description of a new subspecies is justified on the grounds also that this occurrence is allopatric to all occurrences of the nominate subspecies.

Family CYThERURIDAE Müller 1894

Genus *Oeulocytheropteron* Bate 1972

Oeulocytheropteron raybatei McKenzie sp. nov.

Figs 4Q, 6G, H

ETYMOLOGY: For Dr R. H. Bate, British Museum (Natural History).

DESCRIPTION: Carapace small; subquadrangular in lateral view; markedly inequivalved, RV strongly arched dorsally while LV is nearly straight dorsally (cf. Figs 6G, 6H); ventral margin inflexed anteromedially; anterior subacuminate anteroventrally; posterior terminating in a short posterodorsal cauda; eye tubercle small but distinct (generic character); ventral alae prominent; surface micropunctate, with a slender dorsomarginal ridge and other ridges extending from the alae posterodorsally and anteroventrally; greatest height anteromedial, behind the eye spot. Internally: duplicature well developed, moderately broad; radial pore canals few, grouped anteroventrally and also including 2 into the posterodorsal cauda; normal pore canals simple, rimmed; central muscle scars located within the alae, comprising a subvertical row of 4 adductor scars, plus a single frontal scar (all readily visible on the external valve surfaces); hinge artiooperatodont, comprising crenulate terminal projections in the RV, with a crenulate median furrow which is more coarsely crenulate at either end. Sex dimorphism distinct, males relatively lower than females. Soft parts unknown.

DIMENSIONS: Holotype ♀ RV MMC01686 length 0.48 mm, height 0.28 mm. Paratype ♀ LV MMC01685 length 0.46 mm, height 0.24 mm.

TYPE LOCALITY: Coral site at Evans Head, N.S.W. (locality 18, Fig. 1), 0.36-0.55 m.

OTHER LOCALITIES: The species also occurs in samples from the type locality at depths of 0.73-0.91 m, 1.09-1.27 m, 1.45-1.64 m, and 1.64-1.82 m.

REMARKS: As a cytheropteronine taxon, this species would be part of the sublittoral (offshore) assemblage which accounts for the fact that Hartmann (1981) failed to record it from the N.S.W. coast. Of the several New Zealand species described by Hornibrook (1952) it is closest to *O. fornix* but differs from that species by its more pointed alae and better defined dorsal and posterior ridges.

Family Trachyleberididae Sylvester-Bradley 1948

Genus *Keijella* Ruggieri 1967

Keijella jankeiji McKenzie sp. nov.

Figs 5F, 6E, F

ETYMOLOGY: For Dr A. J. Keij, petroleum consultant, Rijswijk, Netherlands.

DESCRIPTION: Carapace medium sized; subovate in lateral view; anterior broadly rounded, posterior less broadly rounded; dorsum gently convex and sloping backwards; venter also weakly convex and inflexed anteromedially; surface ornamented almost all over by large pits (with some indication of a polygonal reticulation posteriorly); also bearing several very short anterior marginal spines and a short, curved posteroventral spine; eye spot depressed; greatest height anteromedial. In dorsal view, subelliptical. Internally: duplicature well developed, moderately broad; radial pore canals rather numerous and straight; normal pore canals simple, celled; central muscle scars comprising 4 adductors in a curved subvertical series (concave anteriorly) plus a broadly V-shaped frontal scar and 2 small mandibulars; hinge powerful, hemiamphodont, comprising a prominent, lobate front tooth behind which is a depression followed by a finely crenulate median furrow leading to a strong lobate posterior tooth. Sex dimorphism present, males relatively more elongate than females. Soft parts unknown.

DIMENSIONS: Holotype ♀ RV MMC01707 length (excluding spines) 0.68 mm, height 0.40 mm.

TYPE LOCALITY: Evans Head, N.S.W. (locality 18, Fig. 1), 0.91-1.09 m.

OTHER LOCALITIES: The species also occurs in samples 1.09-1.27 m, 1.27-1.45 m, 1.64-1.82 m, from Evans Head, and in WRC bores 39101, 39135, 39138, 39139, 39140, 39145, 39149, 39152, 39163, 39165 and the Ambulance Station Bore.

REMARKS: The new species may be compared with the common Indo-Malaysian taxon *K. hodgii* (Brady 1866) originally described from the Levant sponge sand but later also recorded from the Indopacific (Brady 1880, p. 95) and recently figured by McKenzie and Sudijono (1981, plate 3, fig. 6). It differs from that species by being pitted almost all over whereas *hodgii* has scarcely any pits but instead is ridged posteriorly.

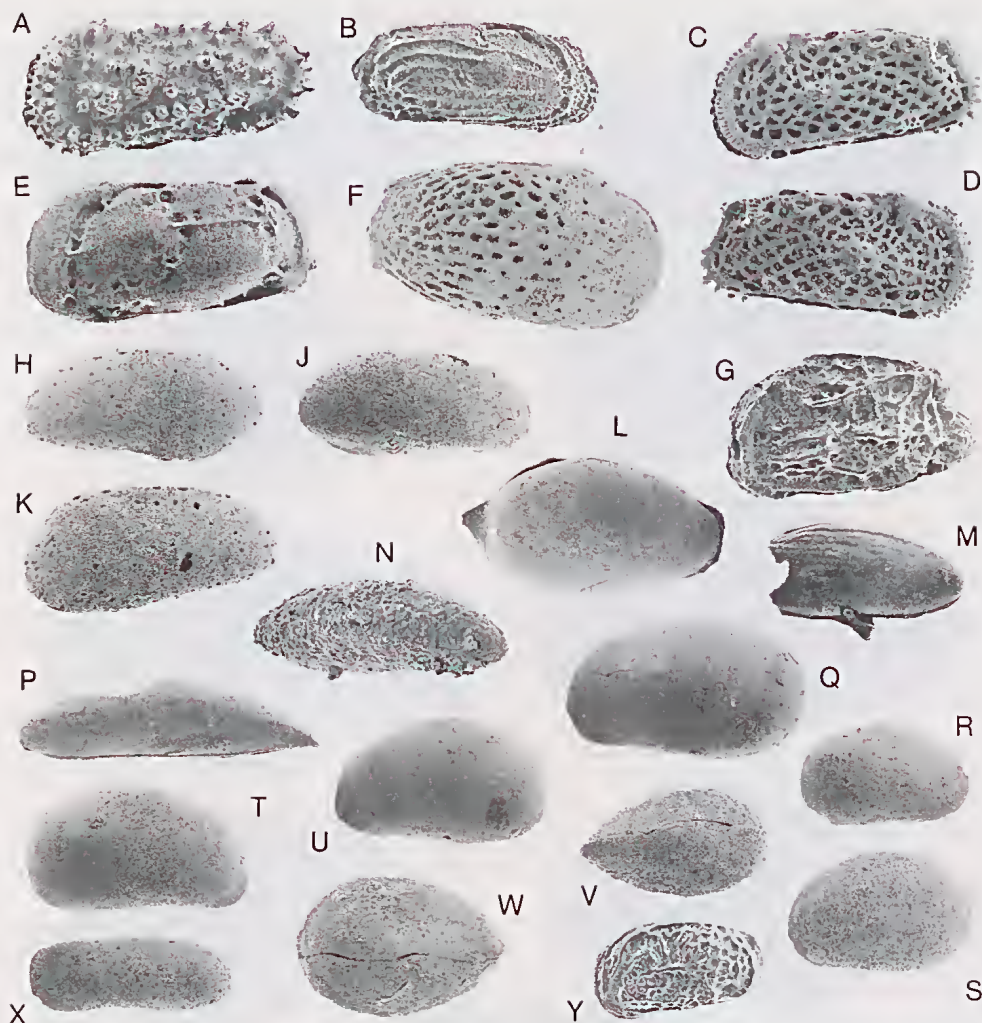


Fig. 5—Representative ostracodes from the Late Pleistocene Gundurimba Clay. Locality numbers refer to Fig. 1. All $\times 50$. A, *Trachyleberis dampierensis* (Hartmann), gerontic σ LV, loc. 5, 20-21 m, MMMC01702. B, *Australimiosella* sp., ϕ RV, loc. 10, 38-39 m, MMMC01703. C, D, *Cletocythereis rastromarginata* (Brady), loc. 5, 20-21 m. C, σ LV, MMMC01705. D, σ RV, MMMC01704. E, *Bradleya* sp., ϕ LV, loc. 8, 19-20 m, MMMC01706. F, *Keijella jankeiji* sp. nov., paratype ϕ RV, loc. 18, 0.91-1.09 m, MMMC01708. G, *Mutilus* sp., ϕ LV, loc. 18, 0.73-0.91 m, MMMC01709. H-K, *Paracytheroma sudaustralis* (McKenzie), loc. 10, 36-37 m. H, ϕ LV, MMMC01712. J, ϕ RV, MMMC01710. K, ϕ RV, MMMC01711. L, *Paradoxostoma evansheadensis* sp. nov., holotype ϕ RV, loc. 18, 0.36-0.55 m, MMMC01713. M, *Paradoxostoma* sp. broken RV, loc. 18, 1.27-1.45 m, MMMC01714. N, ?*Machaerina* sp. σ carapace, loc. 5, 20-21 m, MMMC01716. P, *Machaerina* sp., σ LV, loc. 18, 1.27-1.45 m, MMMC01715. Q-S, *Xestoleberis cedunaensis* Hartmann. Q, ϕ LV, loc. 18, 0.36-0.55 m, MMMC01717. R, juvenile RV, loc. 5, 20-21 m, MMMC01719. S, juvenile RV, same, MMMC01718. T, *Xestoleberis limbata* Hartmann, ϕ RV, loc. 18, 0.36-0.55 m, MMMC01720. U, *Xestoleberis tigrina* (Brady), σ LV, loc. 18, 0.36-0.55 m, MMMC01721. V, *Xestoleberis* sp., carapace, loc. 7, 15-16 m, MMMC01722. W, *Aspidoconcha* sp., ϕ carapace, loc. 10, 36-37 m, MMMC01723. X, *Pseudopsammocythere* sp., σ LV, loc. 7, 16-17 m, MMMC01724. Y, *Callistocythere hartmanni* McKenzie, σ carapace, loc. 17, 14-15.5 m, MMMC01725.

Family PARADOXOSTOMATIDAE Brady & Norman 1889

Genus *Paradoxostoma* Fischer 1855

Paradoxostoma evansheadensis McKenzie sp. nov.

Figs 5L, 6D

ETYMOLOGY: For Evans Head, N.S.W.

DESCRIPTION: Carapace medium sized, subovate in lateral view; dorsum regularly convex; venter nearly straight, weakly inflexed anteromedially and upswept posteriorly; anterior subacuminate anteroventrally; posterior terminating in a small but definite cauda; eye spot distinct, clear; patch pattern of 2 clear patches (the



Fig. 6—New ostracode taxa from the Late Pleistocene Gundurimba Clay. Locality numbers refer to Fig. 1. A, B, *Cytherella loukornickeri* sp. nov., loc. 18, 0.97–1.09 m. A, paratype ♀ RV, MMMC01647, internal view, $\times 75$. B, holotype ♀ LV, MMMC01646, $\times 75$. C, *Cytherella lismorensis* sp. nov., holotype ♂ carapace, loc. 4, 13–14 m, MMMC01648, $\times 75$. D, *Paradoxostoma evansheadensis* sp. nov., holotype ♀ RV, loc. 18, 0.36–0.55 m, MMMC01713, $\times 75$. Specimen slightly damaged prior to re-photography. E, F, *Keijella jankeiji* sp. nov., holotype ♀ RV, loc. 18, 0.91–1.09 m, MMMC01707. E, external view, $\times 75$. F, internal view, $\times 75$. G, H, *Oculocytheropteron raybatei* sp. nov., loc. 18, 0.36–0.55 m. G, holotype ♀ RV, MMMC01686, $\times 100$. H, paratype ♀ LV, MMMC01685, $\times 100$. J–L, *Tanella gracilis minor* subsp. nov., loc. 17, 14–15.5 m. J, internal view of paratype ♂ RV, MMMC01681, $\times 100$. K, paratype ♀ RV, broken, MMMC01680, $\times 100$. L, holotype ♀ RV, MMMC01683, $\times 100$.

anterior patch lying below the eye spot) with the remainder of each valve fuscous; greatest height medial and over half the length (in females). In dorsal view regularly and broadly elliptical, pointed at both ends (more prominently in the rear—an effect of the cauda); greatest breadth medial, about the same as or slightly greater than the height. Internally: the marginal duplicature is well developed and moderately broad, with prominent anterior and posterior vestibules, radial pore canals rather few, short and straight, including 2 into the cauda; normal pore canals simple, rimmed; central muscle scar comprising a subvertical series of 4 adductors but no frontal scar (generic character); hinge adont, consisting of a ridge in the RV and the groove in the LV. Sex dimorphism weak, males relatively more elongate than females. Soft parts unknown.

DIMENSIONS: Holotype, ♀ RV MMMC01713, length = 0.64 mm; height = 0.36 mm, breadth = 0.38 mm (after doubling the breadth of the RV).

TYPE LOCALITY: Evans Head, N.S.W. (loc. 18) 0.36-0.55 m.

OTHER LOCALITIES: The species also occurs in Evans Head samples at 0.55-0.73 m, 1.45-1.64 m and 1.64-1.82 m.

REMARKS: The patch pattern of this species is similar to that of *Paradoxostoma fuscumaculosum* Hartmann 1981 described from Heron Island, Capricorn Group, Great Barrier Reef (Hartmann 1981, pp. 126-127, figs 72-75). The shape of Hartmann's species, however, is elongate ovate and it lacks the posterodorsal cauda of *P. evansheadensis*.

REPOSITORY

All samples are housed in the collections of the Geological and Mining Museum, Sydney. Specimen numbers with the prefix MMMC refer to the microfossil register of that institution.

ACKNOWLEDGEMENTS

We thank Dr L. W. Drury for discussion of many points, and for making available the manuscript of an unpublished article. The samples were made available by the N.S.W. Water Resources Commission. J. W. Pickett publishes with the permission of the Secretary, N.S.W. Department of Mineral Resources. Research on Australian Ostracoda (K. G. McKenzie) is supported by ARGS Grant No. E80 15287.

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APPENDIX

OSTRACODA WITH RESPECT TO DEPTHS—WRC BORES, LISMORE DISTRICT, N.S.W.

Bore No. 39101

- 12-13 m: *Osticythere reticulata* Hartmann 1980; '*Neomonoceratina, koenigswaldi* Keij 1954.
- 15-16 m: *O. reticulata*; '*N. koenigswaldi*'; *Callistocythere hartmanni* McKenzie 1967; *Keijella jankeiji* sp. nov.; *Xestoleberis cedunaensis* Hartmann 1980.

Bore No. 39135

- 15-16 m: *O. reticulata*; *Trachyleberis dampierensis* (Hartmann 1978).
- 20-21 m: *O. reticulata*; *T. dampierensis*; *K. jankeiji*.
- 21-22 m: *Phlyctenophora zealandica* Brady 1880; *O. reticulata*; *T. dampierensis*; *K. jankeiji*.
- 22-23 m: *O. reticulata*; *Callistocythere dorsotuberculata* Hartmann 1980; *T. dampierensis*; *K. jankeiji*.

Bore No. 39138

- 20-21 m: *Propontocypris* sp.; *Loxoconcha trita* McKenzie 1967; *O. reticulata*; 'N'. *koenigswaldi*; 'Pec-tocythere' *portjacksonensis* (McKenzie 1967); *T. dampierensis*; *K. jankeiji*.

Bore No. 39139

- 13-14 m: *Cytherella loukornickeri* sp. nov.; *Cytherella lismorensis* sp. nov.; *Paranesidea* cf. *attenuata* (Brady 1880); *Paracypris bradyi* McKenzie 1967; *Loxoconcha australis* Brady 1880 *minor* Hartmann 1978; *L. trita*; *Hemicytheridea reticulata* Kingma 1948; *Bishopina vangoethemi* Wouters 1981; *O. reticulata*; *Neomonoceratina mediterranea* Ruggieri 1953; *C. dorsotuberculata*; *Callistocythere keiji* Hartmann 1978; 'P.' *port-jacksonensis*; *T. dampierensis*; *Cletocythereis rastrummarginata* (Brady 1880); *K. jankeiji*; *X. cedunaensis*; *Xestoleberis limbata* Hartmann, 1980.

Bore No. 39140

- 10-11 m: Nil.
 11-13 m: *O. reticulata*; *K. jankeiji*.
 13-15 m: *K. jankeiji*.
 15-16 m: *L. trita*; *T. dampierensis*; *K. jankeiji*.
 16-17 m: *C. loukornickeri*; *C. lismorensis*; *N. mediterranea*; *T. dampierensis*; *K. jankeiji*.
 17-18 m: *C. loukornickeri*; *O. reticulata*; *N. mediterranea*; *K. jankeiji*.
 18-19 m: *C. loukornickeri*; *N. mediterranea*; *K. jankeiji*.
 19-20 m: *C. loukornickeri*; *O. reticulata*; *T. dampierensis*; *K. jankeiji*.
 20-21 m: *C. loukornickeri*; *C. lismorensis*; *P. cf. attenuata*; *P. bradyi*; *P. zealandica*; *L. australis minor*; *L. trita*; *cytherurid?* sp. juv.; *O. reticulata*; 'N'. *koenigswaldi*; *N. mediterranea*; *Parakrithella australis* McKenzie 1967; *C. dorsotuberculata*; *C. keiji*; *Tanella gracilis* Kingma 1948; *T. dampierensis*; *C. rastrummarginata*; *K. jankeiji*; *Paracytheroma sudaustralis* (McKenzie 1978); *Machaerina* sp.; *X. cedunaensis*.
 21-22 m: *C. loukornickeri*; *P. zealandica*; *Propontocypris* sp.; *L. australis minor*; *L. trita*; 'N'. *koenigswaldi*; *T. dampierensis*; *X. cedunaensis*.

Bore No. 39143

- 17-18 m: *C. keiji* (fragment).
 20-21 m: *P. cf. attenuata*; *P. bradyi* (fragment); *B. vangoethemi*; *C. dorsotuberculata*; *Ponticythereis militaris* (Brady 1866); *T. dampierensis*.

Bore No. 39145

- 15-16 m: *Xestoleberis* sp.
 16-17 m: *C. loukornickeri*; *K. jankeiji*; *Pseudopsam-mocythere* sp.
 17-18 m: *C. lismorensis*; *P. zealandica*; *L. australis minor*; *L. trita*; *B. vangoethemi*; *O. reticulata*; 'N'.

koenigswaldi; *C. dorsotuberculata*; *Callistocythere purii* McKenzie 1967; *T. dampierensis*; *K. jankeiji*; *X. cedunaensis*.

- 19-20 m: *L. trita*; *T. dampierensis*; *K. jankeiji*.
 20-21 m: *K. jankeiji*.
 21-22 m: *K. jankeiji*.
 22-23 m: Nil.

Bore No. 39149

- 19-20 m: *C. loukornickeri*; *C. lismorensis*; *P. zealandica*; *L. trita*; *H. reticulata*; *P. australis*; *T. dampierensis*; *Bradleya* sp. (juv.); *K. jankeiji*; *X. cedunaensis*.

Bore No. 39150

- 33.5-33.6 m: Nil.

Bore No. 39152

- 35.25-36 m: *C. loukornickeri*; *C. dorsotuberculata*; *K. jankeiji*.
 36-37 m: *L. australis minor*; *T. dampierensis*; *P. sudaustralis*; *Aspidoconcha* sp.
 37-38 m: Nil.
 38-39 m: *C. loukornickeri*; *T. dampierensis*; *Australimoo-sella* sp.

Bore No. 39155

- 40-41.5 m: *C. loukornickeri*; *T. dampierensis*.
 41.5-43 m: Nil.
 63-64.5 m: Nil.

Bore No. 39157

- 25.5-26 m: *O. reticulata* (fragment).
 26-27.5 m: Indet. fragment, possibly *Loxocythere* sp.
 27.5-29 m: *O. reticulata*.
 29-30.5 m: Nil.
 30.5-33 m: Nil.

Bore No. 39158

- 29-30.5 m: *O. reticulata*; 'N'. *koenigswaldi*.
 35.5-37 m: *O. reticulata*; 'N'. *koenigswaldi*.
 37-38.5 m: *H. reticulata*.
 38.5-40 m: Nil.

Bore No. 39163

- 3-4.5 m: *K. jankeiji*.
 4.5-6 m: Nil.

Bore No. 39165

- 18.5-20 m: *C. dorsotuberculata*; *T. rugibrevis*.
 20-21.5 m: *T. dampierensis*; *K. jankeiji*.

Lismore Ambulance Station Bore

- 14-15.5 m: *L. trita*; *O. reticulata*; 'N'. *koenigswaldi*; *C. hartmanni*; *Tanella gracilis* Kingma 1948 *minor* subsp. nov.; *K. jankeiji*.

- No Depth *P. zealandica*; *L. trita*; *O. reticulata*; 'N'.
 Indicated: *koenigswaldi*; *K. jankeiji*; *P. sudaustralis*.

Localities Unknown

- 12-13 m: *O. reticulata*.
 15-16 m: *O. reticulata*.
 33.5-33.6 m: Nil.



S1321

